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June 17, 1911

THE GENUS *GYROCOTYLE*, AND ITS
SIGNIFICANCE FOR PROBLEMS
OF CESTODE STRUCTURE
AND PHYLOGENY

BY

EDNA EARL WATSON



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* A dissertation presented to the Faculty of the College of Natural Sciences, in the University of California, in partial satisfaction of the requirements for the degree of Doctor of Philosophy. April, 1910.

A. INTRODUCTION.

The Cestodaria (Monticelli, 1892) or monozoic cestodes (Lang, 1891), including *Amphilina*, (Rud.), *Archigetes* (Ratz) *Caryophyllaeus*, (Rud.) *Gyrocotyle*, (Diesing) and *Wageneria* (Wag.) are of peculiar interest to students of the platyhelminths. They occupy a position intermediate between the merozoic cestodes and the trematodes, being allied to the latter by the general arrangement of the reproductive organs and by their fundamentally unitary character, and distinguished from them by the absence of a digestive tract. This last characteristic allies them with the merozoic cestodes, from which they are distinguished on the other hand by their unsegmented condition and by the accompanying absence of segmental repetition of the genital organs, as stated by Monticelli (1892). The group is difficult to consider as a whole because of the remarkable diversity shown in its four well-established genera, both as to structure, life-history and host. The characters mentioned above practically exhaust those common to the group, and each genus possesses characters of such rank as fittingly to receive ordinal distinction in classification. Two of the genera, *Archigetes* and *Wageneria*, have but one species each. Two each have been assigned to *Caryophyllaeus* and *Amphilina*, and at least four are now recognized in the genus *Gyrocotyle*. The grounds on which specific distinctions have been made are far from satisfactory. These considerations indicate that the group is not only phylogenetically intermediate but composed of very old, long-established forms, on which the forces that make for speciation have long since ceased to act. The Cestodaria are either remnants of a once large and differentiated group, or they are members of a class never differentiated to any considerable extent. They are presumably of greater age than the cestodes, their hosts being invertebrates or primitive vertebrates. Cestodes are phylogenetically the youngest of the platyhelminths, since the host in the sexual period is always a vertebrate. They have been greatly and variously modified by their parasitic habit, and they present problems of structure and development of extreme difficulty. It seems probable that much help towards the solution of these can

be obtained through an exhaustive study of the Cestodaria, the nearest surviving relatives of the merozoic cestodes; and in this possibility lies the chief interest pertaining to the former group and to this investigation.

Lönnberg (1897), in a study of the phylogeny of parasitic platyhelminths, discusses the possible phylogenetic significance of the Cestodaria and comes to the conclusion that they cannot be regarded as ancestral forms of the merozoic cestodes:

"Die jetzigen polyzoischen Bandwurmstrobilen sind natürlich aus monozoischen Formen hervorgegangen. Die noch jetzt existierenden monozoischen Cestoden können aber kaum als Stammformen der polyzoischen angesehen werden. . . . Diese [*Gyrocotyle* and *Amphilina*] sind wahrscheinlich beide ursprünglich, weichen aber in mehreren Hinsichten von den echten Cestoden recht sehr ab. *Gyrocotyle* ist durch das Erweben von Haftorganen an beiden Körperenden, das Trichterorgan am Vorderende und das Acetabulum am Hinterende, unfähig geworden, sich weiter zu entwickeln."

While the writer is convinced of the essential correctness of Lönnberg's general contention, that the ancestors of cestodes must be sought, not among Cestodaria or trematodes, but among Turbellaria, it is felt that he undervalues the evolutionary significance of the Cestodaria. The merozoic cestode is probably not the descendant of any monozoic cestode now in existence; but because of the fundamental similarity between the two groups we may hope to find, in the simpler forms meeting the same problems in essentially the same way, some clue to the manner in which occurred the complicated processes by which the hypothetical turbellarian-like ancestor was transformed into the merozoic cestode. Naturally, those cestodes which are secondarily monozoic, *Archigetes* and *Caryophyllaeus* (Lönnberg, 1897) are of little value in this sense. *Amphilina* (*Acipenser*) and *Gyrocotyle* (*Chimaera*) are primarily monozoic, inhabit hosts of great phylogenetic age, and show fundamental correspondence to the typical cestode structure in all important respects. *Gyrocotyle*, the genus with which this paper is concerned, Lönnberg regarded as off the line of cestode evolution, side-tracked by the development of organs of attachment at both ends. The writer hopes to show that only one functional organ of attachment is present, that this is homologous to the cestode scolex, although

much simpler, and that its structure and position afford very significant indications of the origin and primitive location of the cestode scolex. The evidence of this homology and its theoretical significance will be discussed later; the point of chief interest now is that the very structural peculiarity which Lönnberg regarded as removing *Gyrocotyle* from any great phylogenetic interest is the source of its most significant and interesting contribution to the solution of the problem of cestode origins.

This investigation has been carried on in the Zoological Laboratory of the University of California and at the Station of the Marine Biological Association at La Jolla. For material I am indebted to Professor C. A. Kofoid, and through him to the United States Bureau of Fisheries and the Marine Biological Association at La Jolla; also to Professor Jacques Loeb, for privileges at the Herzstein Research Laboratory at Monterey. For substantial assistance in the preparation of drawings for publication I am indebted to Miss E. J. Rigden. For the pointing out of this line of investigation, for help in obtaining the obscure and not easily accessible literature of the subject, and for counsel and encouragement, I wish to express my debt to Professor Kofoid, under whose direction this work has been brought to its present state of completion.

B. HISTORY OF THE GENUS.

The history of the genus *Gyrocotyle* is complicated by conflicting reports as to its systematic position, its habitat, its orientation and its morphology. The genus was established by Diesing (1850), for a parasite obtained by Gueinzius in 1842 from *Antilope pygarga*, a South African ungulate. This report was an error (Diesing, 1858, p. 492), but was accepted as correct for several years, contributing in no small degree to the confusion concerning the habitat and systematic position of the genus. In 1844 Kröyer showed Diesing a parasite similar to that collected by Gueinzius, taken from inside the shell of an edible mollusk (Diesing, 1855). These two specimens were grouped in one species by Diesing (1850) under the new genus *Gyrocotyle*, and described in the following terms:

"Corpus sub-ellipticum depresso; os subterminale corpore continuum; os subterminale anticum exiguum; acetabulum unum in extremitate caudali terminale, sessile, orbiculare, disce in gyros plicata; penis ventralis superus lateralis; apertura feminea infra penem centralis; porus excretorius dorsalis supra acetabulum." [Quoted from Braun (1889)].

The genus as thus defined contained only a single species, *Gyrocotyle rugosa*. Diesing referred the genus to the trematodes, placing it near the genus *Amphistomum* because of the posterior position of its acetabulum. In 1855, in his description of the collection of endoparasitic worms made by Natterer in Brazil, Diesing published a second description of the genus identical with the first, with five figures and a discussion of the habitat and systematic affinities of the genus. He regards it as improbable that both *Mactra edulis* and *Antilope pygarga* are true hosts of *Gyrocotyle*, and believes that the report of its occurrence in *Mactra* is an error. In case *Mactra* should prove to be the true host, he concludes that *Gyrocotyle* as an ectoparasite would have to be referred to the Bdellidea. As an endoparasite of *Antilope*, he places it under the trematodes. Diesing made no attempt at a study of the internal structure of the parasite and apparently only a cursory examination of its external appearance. From his figures it seems probable that his specimens were in a state of decomposition when preserved.

In 1852 Wagener described and figured a parasite found by himself and Grube in the spiral valve of *Chimaera monstrosa*, at Nice. For this he established the genus *Amphiptyches*, containing a single species, *urna*, and referred this genus to the cestodes because of its morphological resemblance to that group. Wagener made a careful study of the internal structure of the worm, both in the living animal and preserved specimens made partially transparent by clearing. Except for confusion as to the ducts of the genital organs and in a few minor details, his figures are correct. Diesing's (1855) description and figures convinced Wagener that *Amphiptyches* was identical with *Gyrocotyle*. In a letter to Diesing (1857) he calls the latter's attention to *Amphiptyches urna*, and in his "Enthelminthica No. V." (Wagener, 1858), he discards *Amphiptyches* as a generic name and retains it as a specific name for the form discovered by him:

Gyrocotyle amphiptyches. Diesing ("Revision der Myzhelminthen," 1858) recognizes *Amphiptyches* as a distinct genus, placing it near *Amphistomum* under trematodes, in the place occupied in his earlier paper (1855) by *Gyrocotyle*, then considered an ectoparasite of *Antilope pygarga*. He supposes *Amphiptyches* to have a mouth, digestive tract and anus, in the face of Wagener's (1852, p. 547) explicit statement to the contrary. He gives as its habitat the gills and intestinal tract of *Chimaera monstrosa*. His own genus, *Gyrocotyle*, he puts under the Bdellidea near *Malacobdella* (Diesing, 1858, p. 492). He makes certain changes in the generic description, the most important of these being in the interpretation of the ventral canal opening (proboscis of Spencer); in his description of 1850 he regards it as an excretory pore, in 1858 as the anus. The change was made in order to place the genus under the Bdellidea, where Diesing was convinced it belonged if *Mactra* was its true host. That the report of its occurrence in *Antilope* was an error Diesing had discovered in the interval between 1855 and 1858, and it was probably due to this discovery that the change in the position of the genus was made (Diesing, 1858, p. 492).

Diesing's disposition of *Amphiptyches* was apparently not satisfactory to Wagener, for in his paper "Ueber *Amphilina foliacea*, *Gyrocotyle* Diesing und *Amphiptyches* (Grube and Wagener)" (1858), Wagener definitely withdraws *Amphiptyches*, recognizing his form to be a species of Diesing's older genus. In Diesing's "Nachträge und Verbesserungen zur Revision der Myzhelminthen" (1859), he agrees with Wagener in placing the two species under one genus, which he refers to the "Bdellidea monocotylea."

The two species are distinguished one from the other only by the absence of spines and lateral frills and the smaller size of the "tail rosette" in *Gyrocotyle rugosa*.

Diesing (1859, p. 448) regards the genus as typically ectoparasitic on marine mollusks, assuming that the species of Grube and Wagener has its normal habitat, not in *Chimaera monstrosa*, but rather on some of those mollusks whose fragments occur in the intestine of the fish. "Da *Gyrocotyle rugosa* aus einem

Mollusken, nämlich der *Mactra edulis* stammt, so ist es sehr wahrscheinlich, dass auch die von Grube und Wagener beschriebene Art ihren eigentlichen Wohnort nicht in der *Chimaera monstrosa*, sondern vielmehr in einer jener Mollusken, deren Fragmente sich im Darme des Fisches verfanden, habe."

Van Beneden and Hesse (1864), maintain the two genera and refer both to the Hirudinea as the "Malacobdellaria dioici." These authors agreed with Diesing in regarding a mollusk as the true host of *Amphiptyches*, stating explicitly that it is not to be considered a parasite of *Chimaera*, but as having been taken in by chance with the mollusk on which the fish feeds. Later Van Beneden (1869) withdrew from this position and classed *Amphiptyches* as a true parasite of *Chimaera*.

No further work was done on either of these forms until Monticelli's "Saggio di una morfologia dei trematodi" (1888) in which he excludes *Gyrocotyle* and *Amphiptyches* from the trematodes, referring *Gyrocotyle* to the bdelloides, near *Malacobdella*, following Hesse and Van Beneden. He affiliates *Amphiptyches* with the cestodes, suggesting that *Amphilina* and *Amphiptyches* are closely related forms, the latter being the simpler of the two, and together should be regarded as forms transitional between trematodes and cestodes. Shortly after this Monticelli (1889b) compared the specimens of *Gyrocotyle* and *Amphiptyches* available in the museums of Leipzig, Berlin and Vienna. As a result of the comparison he says:

"Io ho potuto stabilire con certezza la loro posizione sistematica desumendola dai loro caratteri anatomici ed embryologici. Dalle mie ricerche sono pervenuto alle seguenti conclusioni:

"1. Che l' *Amphiptyches* ed il *Gyrocotyle* devono considerarsi, come già pensavano il Wagener ed il Diesing, due specie distinte del gen. *Gyrocotyle*. Le due specie si chiameranno: *G. rugosa* Diesing e *G. urna* Grube e Wagener.

"2. Che il gen. *Gyrocotyle* deve allogarsi fra i Cestodi e riguardarsi affine all' *Amphilina*."

He goes on to say that the first conclusion rests on remarkable uniformity of structure; the sole external difference being the lack or slight development of the lateral folds in *Gyrocotyle*. The second conclusion rests on the mode of development and internal structure of both species. The similarity of cestodarian

organization to that of the cestodes is then pointed out in the musculature, the lack of a digestive tract, the arrangement of the excretory system, the general form of the nervous system, the arrangement of the genital organs, and the presence of a six-hooked embryo, in *Gyrocotyle rugosa*.

In the same year (1889c), in examining the Entozoa of the British Museum, Monticelli found an undoubted example of *G. rugosa*, taken from *Callorhynchus antarcticus* at Dunedin, New Zealand. As he points out (1890), *G. rugosa* had up to this time been reported only from *Mactra edulis*, *G. urna* only from *Chimaera monstrosa*. He summarizes his conclusion as follows:

"1. Che il genere *Gyrocotyle* è parassita proprio della famiglia delle Chimaeridae.

"2. Che i due generi finora conosciuti della famiglia (*Chimaera* e *Callorhynchus*) albergano ciascuno una specie del genere *Gyrocotyle*.

"3. Che il genere *Gyrocotyle* perviene nelle Chimaeridae per mezzo di molluschi bivalvi."

Monticelli discusses the question whether *Mactra edulis* is to be regarded as the true intermediate host of *G. rugosa*, and concludes that, since the example found in the mollusk contained hooked embryos, a third host must be found to convey *G. rugosa* to *Mactra*. He suggests that possibly some of the mollusks on which *Chimaera monstrosa* feeds (probably some member of the *Cyprinidae*), may be the intermediate hosts of *G. urna*.

This work of Monticelli's definitely settles the question as to the generic identity of *Gyrocotyle* and *Amphiptyches*, and establishes two species of the genus *Gyrocotyle*, separated by three distinct characters. Further, it indicates that *G. rugosa* is a true parasite of *Callorhynchus*, though this point could hardly be considered as established by a single occurrence of the parasite in the fish.

Further evidence on this question was supplied by Spencer's (1889) report on the morphology of three specimens of *Gyrocotyle* found by him in the mouth of a specimen of *Callorhynchus antarcticus*. These Spencer referred to Wagener's *Amphiptyches urna*, but from the form of the lateral frills and the presence of hooked embryos, it seems quite clear that his species was not *G. urna*, but *G. rugosa*. (See my pl. 38, fig. 36). This

view is substantiated by Monticelli's identification of a specimen from *C. antarcticus* as *G. rugosa*, Diesing's original species, though the size, number and character of the frills of the terminal rosette as figured by Spencer do not agree with Diesing's original figure of those structures.

Braun (1889) published a careful review of the literature of the genus up to and including Monticelli's (1890) paper on the finding of *Gyrocotyle rugosa* in *Callorhynchus antarcticus*, but not including Spencer's paper. He reduces *Amphiptyches* to a synonym of *Gyrocotyle*.

Lönnberg (1890a) mentions the finding of *Gyrocotyle* in July and August, near Bergen. He later (1890b) published a short paper, "Ueber *Amphiptyches* Wag. oder *Gyrocotyle urna* (Grube et Wagener) Diesing." In a subsequent paper (1891) he includes a detailed study of *Amphiptyches urna*, covering the questions of synonymy, systematic position, occurrence, habitat, behavior, orientation, and morphology, concluding with a comparison of *Amphiptyches* with the other genera of the Cestodaria. Lönnberg agrees with Wagener in regarding *Gyrocotyle* as a true cestode; he considers it the most primitive of the monozoic cestodes and the most closely related to the trematodes. He does not accept the combination of *Gyrocotyle* and *Amphiptyches* in one genus, and regards the form investigated by him, from *Chimaera monstrosa*, as *Amphiptyches urna*. Aside from his careful study of this species, which will be referred to later, Lönnberg's most important contribution to the knowledge of the genus was his description of the animal in the living condition and the various forms assumed by it. Its behavior and appearance he describes as being in the majority of cases similar to that described by Wagener, namely, pointed at one end, with marginal frills and a terminal rosette. But this typical body-form he saw transformed into a totally different one in which the worms "ganz platt und am beiden Enden gleich sind" (p. 17). (See my pl. 33, figs. 1-4). The ordinary frilled form he regards as a contracted condition of this "Ligulaähnlicher" worm; the intermediate stage between the two he describes as one in which "die Seitenränder in grossen Wellen gebogen sind und nur der äusserste Teil des Trichters in einen kleinen krausen

Kopf zusammengezogen." He describes also a third contraction stage, differing from the ordinary frilled stage even more widely than the "Ligulaähnlicher." This is the most expanded state of the worm, described by Lönnberg as follows:

"Wenn der *Amphiptyches* sich lebhafter bewegen will, verlängert er sein Körper: die Querrunzeln an der Mitte des Körpers glätten sich aus, die dichten seitlichen Krausen wandeln sich dann zuerst in weniger zahlreicher Falten um und diese gehen darauf in einige wenige grosse Wellen über, die bald auch verschwinden und die Seitenränder glatt erscheinen lassen. Der Körper ist nun im Ligulastadium, also platt und lanzettentümlich. Aber gleichzeitig hiermit vollziehen sich am Trichter und dem Halsteil grosse Veränderungen. Dieser verliert seine seitlichen Falten, wird länger und schmäler und erhält eine cylindrische Form. Jener verlängert sich unverhältnismässig mehr und zwar in der Weise, dass er von hinten und vorwärts sich in ein cylindrisches Rohr umwandelt, der krause 'Kopf' wird immer kleiner und gleichwie vorwärts geschoben; dies geht natürlicher Weise so zu, dass nach un nach mehr von den proximalen Teilen des Trichters zur Bildung des cylindrischen Rohres angewandt werden; bald sind nur die äussersten Lippen ein wenig kraus und schliesslich werden auch diese glatt und man hat eine solche eigentümliche Form, wie fig. 36 [my pl. 33, fig. 2] zeigt, vor sich. Bei höchster Ausdehnung hat dieser Cylinder, wie oben geschrieben ist, beinahe dieselbe Länge wie der ganze übrige Körper, in welchen er allmälig ohne Absatz übergeht. Es ist mir mit schnell totenden Reagentien gelungen einige Tiere in diesem Stadium zu fixieren, und wenn ich sie mit den gewöhnlichen, krausen Formen vergleiche, muss ich gestehen: hätte ich nicht selbst mit eigenen Augen die Umwandlungen gesehen und die Zwischenstadien studieren können, so würde es mir kaum klar werden können nur zwei verschiedene Kontraktionszustände vor mir zu haben." (Lönnberg, 1891, p. 17.)

These statements of Lönnberg's are in part corroborated by the observations of Professor Collett (quoted in Lönnberg, 1891, p. 17, footnote): "Dass zwei verscheidene Cestoden die Spiralklappe Chimaeras bewohnte und zwar ein platter Ligulaähnlicher und der gewöhnliche krause *Amphiptyches*." In addition Olsson (1896) reports that among thirty-three individuals he found "Deux exemplaires, longs de 30 mm, avaient la forme curieuse qui a été dessinée par Lönnberg (1891, fig. 36) et la conservent encore en alcool. La longueur du cylindre creux, qui est formé du cou et de l'entonnoir, est de près de 13 mm, celle du corps n'est que de 17 mm." (See Olsson's fig. 9, p. 509).

Braun (1894) gives a review of the Cestodaria, including *Gyrocotyle*. He recognizes two species of the genus, *G. urna*

(Gr. et Wag.) (from *Chimaera monstrosa*) and *G. rugosa* Diesing (from *Callorhynchus antarcticus*), but adds (p. 1157) that they "differen so wenig von einander, dass es fräglich ist, ob die Unterscheidung zweier Species sich rechtfertigen lässt; möglicherweise bestehen Unterscheide in der Lage der Genitalpori." According to Lönnberg and Wagener, the vaginal opening is the most anterior and lateral to the penis; but according to Spencer, dealing with *G. rugosa*, the penis opening is anterior to the vagina and marginal.

Benham (1891) recognized the single genus, *Gyrocotyle*, "in the intestine of *Chimaera* and *Callorhynchus*."

Haswell (1902) reported a new species of *Gyrocotyle*, *G. nigrosetosa*, from a new species of *Chimaera*, *C. ogilbyi*, trawled off the Australian coast by the "Thetis." Haswell had one specimen of *G. rugosa*, and two specimens of the new species, "not in good condition for investigation." He did not study the living form. He distinguishes *G. rugosa* from *G. urna* (following Lönnberg's description of the latter) on the following grounds:

- (1) Relative positions of the apertures of the penis and vagina.
- (2) Presence of an eversible cirrus, adapted to self-impregnation, in *G. rugosa*.
- (3) Spinules lining ejaculatory duct, in *G. urna*.
- (4) Size of eggs.
- (5) Presence of hexacanth embryo in *G. rugosa*.
- (6) Shape of spines, which are simpler in *G. rugosa*.

C. GYROCOTYLE OF THE COAST OF CALIFORNIA.

I. OCCURENCE AND HOST.

As this review of the literature shows, the genus *Gyrocotyle* includes three species, *G. rugosa*, *G. urna*, and *G. nigrosetosa*, all occurring as intestinal parasites in the family Chimaeridae. The occurrence of a form of the genus in *Chimaera colliei*, found off the coast of California, has not to my knowledge been previously reported. So far as can be determined, no work has ever been done on the parasites of *C. colliei*. This is the only species

of *Chimaera* found on the Pacific coast of the United States (Dean, 1906, pp. 6, 7) and was first described by Lay and Bennet, 1839, p. 71, pl. 23, in *Zoology of Captain Beechey's Voyage*. Professor Bashford Dean (1906) bases his work largely on eggs of *C. colliei*, and gives a description of the living fish, with notes on its occurrence, habitat, food and breeding habits. It occurs in depths of from 5 to 10 fathoms, being found in shallower water in the Puget Sound region than along the California coast. The specimens examined by the writer have come from the fishing grounds off Piños buoy in Monterey Bay, mentioned by Dean (1906, p. 15); from Cabral's banks off San Diego; and to the north of San Diego, off La Jolla, in depths up to fifty fathoms.

Dean's observations (1906, p. 20) on the food habits of this species, are as follows:

"In view of the special character of the dentition of *Chimaera*, one would naturally expect its food supply to be definite in character. The examination of the contents of its gut, however, showed (*C. colliei*) singularly omnivorous habits. It is true that the broken shells of mollusks are commonly found, as well as fragments of good-sized crustaceans, as indeed the scanty literature records. Thus, in the gut of *C. monstrosa* Faber finds Crustacea and shell-fish fragments; Monticelli, quoting Lütken, *Cyprina islandica*; and Olsson, broken shells (*Leda* and *Venus*) and bits of large decapods. Olsson finds also (and his observations are the most detailed hitherto published on the feeding of *Chimaera*) chaetopods, amphipods, echinoids and polyps. In *C. colliei* observations on about a score of individuals showed a singular mixture of foods. The most numerous were vertebral columns of small isospondylous fishes, a few mollusk shells, usually greatly crushed, a quantity of sand and fine gravel, squid, nudibranchs and opisthobranchs, bits of eases, jaws and setae of annelids, and occasionally a fragment of a crustacean. In one instance the gut was filled with seaweed. One is not surprised, therefore, that this species is taken readily with various baits."

The observations on stomach contents made by Professor Kofoed and myself yield results agreeing in general with the above; with the addition that the stomachs contained a great quantity of echinoderm spines, plates, etc. Small fish were common, as were fragments of lamellibranchs, nudibranchs and gasteropods. Cephalopod beaks were almost always found. Crustacean fragments, especially of *Hippa* and *Blepharada*, were not uncommon in the San Diego specimens. The fish is so nearly omnivorous in food habits that no definite clue as to the life-history of its parasites can be obtained from these data.

The examination of *C. colliei* for parasites has yielded the following results:

(1) The fish is almost invariably infested with a parasite belonging to the genus *Gyrocotyle*. The parasite was found in 34 of the 38 specimens examined.

(2) The parasite rarely occurs singly, but usually two individuals in one host. More than three in one fish I have never found. In four cases a single individual was found.

(3) No other adult cestodes have been found in the alimentary tract of the fish. Encysted cysticerci are common in the walls of the tract, in the mesenteries, liver, etc., especially during the summer months. Parasitic crustaceans were frequently found on the gills, and an aspidocotylean, probably belonging to the genus *Macraspis*, was found embedded in the muscles of the rectum. A distome, bearing a strong superficial resemblance to a small *Gyrocotyle* without frills, was found once in the posterior region of the rectum, and once in the body-cavity.

(4) Two distinct species of *Gyrocotyle* are found in *C. colliei*; one, the less common of the two, is closely related to and perhaps identical with, *Gyrocotyle urna*; the other differs in several characteristics from any species heretofore described. The incompleteness of the figures and descriptions of *G. urna* make it impossible to determine accurately the identity of the form first mentioned with *G. urna*. It will be referred to as *G. urna* (var.?). The second form, which, in view of its well-defined peculiarities and of the absence of any intermediate forms linking it to any described form, I regard as a new species, will be referred to as *G. fimbriata*.

Gyrocotyle fimbriata, sp. nov.

Diagnosis.—Color, creamy white; length 30-55 mm.; width 7-12 mm.; rosette posterior, folds complex; lateral frills 3-5 mm. deep, much folded, passing into smooth lateral fin near anterior extremity; spines numerous, distributed in definite pattern, points directed anteriorly; eggs about 0.09 mm. in average long diameter, no hooked embryos; penis opens mediad of vagina, at about the same antero-posterior level. Occurs in spiral valve of *Chimaera colliei*; can leave host and live for some days free.

These two species occur in fish from the same locality, even taken on the same trawl. Both species have never been found in the same individual. *G. fimbriata* is the more abundant of the two.

II. GROSS ANATOMY OF GYROCOTYLE.

The characteristics on the basis of which species are separated, as given in the literature of the genus, are of various degrees of usefulness and trustworthiness. This is due in great measure to the manifold changes in form and appearance of the living animal and of specimens preserved by different methods in all stages of contraction and deterioration. Before they can be intelligently considered, a brief description of the gross structure of the animal and of the external form and behavior of the living specimen will be necessary. First, the orientation adopted in this paper must be defined. The pointed acetabular end is the anterior, the rosette or canal end the posterior. The surface on which lie the uterine pore and opening of the canal is the creeping surface and the one to which the animal returns in rest. It is therefore ventral. The following description refers especially to *G. fimbriata*.

The worm when alive and attached is almost translucent. After detachment it becomes opaque, whitish-yellow in color, decidedly deeper in tone in the marginal frills and the folds of the terminal posterior rosette. The anterior end is not frilled, is highly contractile, and in the living animal is in constant motion (pl. 33, figs. 7-9). It consists of a very muscular acetabulum, whose margin can be retracted somewhat, while the whole can be drawn back into the body by the retraction of the longitudinal muscles attached to the sucker. Posterior to the acetabulum, in the median dorsal line, lies the opening of the uterus (*ut. po.*, pl. 39, fig. 42). Anterior to this, one-third of the distance between the uterine pore and the posterior margin of the acetabulum, lie the vaginal opening (*vag. op.*), on the ventral surface, and the penis opening (*p. op.*), on the dorsal surface. Both lie almost on the margin, but the penis opening is the more mediad and anterior to the vaginal pore. In the median third of the body of the adult, the much coiled and distended uterus occupies

most of the space. In front and to either side of it, running forward to the posterior margin of the sucker, are the follicles of the testes. Peripheral to these, running out into the lateral folds, are the follicles of the vitellaria, distributed from the acetabular region to the base of the posterior rosette. Along the dorsal surface and to the left of the uterus runs the vagina, leading to the large receptaculum seminis (*rec. sem.*) located just posterior to the uterus. On each side of the receptaculum seminis lie the follicular ovaries (*ovar.*); immediately in front of it are the vitelline ducts (*vit. d.*) and the first coils of the uterus. The shell-glands (*sh. gl.*) are found around these ducts. It is in this region that the ova are fertilized, unite with the yolk-cells and receive their shell-coating. Behind the receptaculum seminis and the ovaries lies the ventral opening of the rosette canal. This structure may be regarded as consisting of two parts. The first is a flaring "funnel," its opening terminal, its margin frilled and folded till it resembles a carnation, or as the Germans put it, a "Kohlkopf." This funnel passes directly acetabulad; it leads into a narrow canal, which turns at almost a right angle to the course of the funnel, passing to the ventral surface (pl. 34, fig. 15). This ventral opening I have called the "canal opening" (*can. op.*, pl. 46, fig. 76), in distinction from the terminal funnel opening above described. Funnel and canal together are called by German workers the "Trichter"; Spencer speaks of the funnel-margin as the "rosette" and calls the canal opening the "proboscis."

Gyrocotyle fimbriata (pl. 48, figs. 80, 81), while bearing a general resemblance to the described species of the genus, differs markedly in certain external characteristics. The body in expanded condition is about four times as long as wide; the lateral frills never totally disappear in any stage of expansion, but can be distinguished from the median portion of the body under all conditions. They are about one-fourth the total width of the body in depth. In contracted specimens the folds of the two sides are invariably drawn toward each other on the ventral (canal opening) surface. The posterior terminal rosette (*post. ros.*, pl. 34, figs. 10, 12-15), is from one-half to three-quarters the greatest width of the body in transverse diameter. Its depth is

about one-third its width, and its dorso-ventral diameter varies from one to one-half the transverse diameter, or even, in exceptional cases, to twice this diameter. The folds of the rosette are not simple, but are secondarily folded, standing in marked contrast to the lateral folds, which consist of a single series of undulations. The appearance suggests that the outer wall of the funnel is more contractile than the inner, the result being the production of a multitude of small secondary folds on the inner surface of the funnel. The gross appearance of this type of rosette suggests a finely villous surface, such as an intestinal mucosa. The large folds with long axis parallel to the long axis of the body, so prominent in other species, are almost obliterated here, especially in preserved specimens.

The anterior or acetabular extremity (pl. 33, figs. 7-9; pl. 36, figs. 22, 23), is bluntly pointed and bears a lateral "fin" of tissue, to a point about half-way to its tip. The acetabulum (*acet.*) is contractile within itself to a high degree and the structure as a whole can be drawn back into the body by the strong longitudinal muscles. This occurs in the most strongly contracted stage (*acet.*, pl. 34, fig. 10). The body is markedly asymmetrical, owing to the formation of a deep "genital notch" in the left margin (*gen. notch*). The vaginal opening lies at the angle of this notch on the ventral (canal opening) surface, appearing as a narrow slit bounded by a slightly elevated ring; the penis opens dorsally in a pit at the base of a very low and inconspicuous mound, about two-thirds of the distance from the apex of the notch to the median line (*p. op.*, pl. 36, fig. 23). The relation of penis to vagina varies within narrow limits, but in general they may be said to be at practically the same antero-posterior level.

The lateral frills extend anteriorly to about the level of the genital notch, in front of which they are continued as the unfrilled "lateral fin" above mentioned. Posteriorly they extend to the tip of the posterior rosette. The funnel, whose margin is formed by the posterior rosette, narrows rapidly to a small canal, which turns at an angle slightly greater than 90° , and opens by a small aperture on the ventral (vaginal opening) surface (*can. op.*, pl. 46, fig. 76). The margin of the aperture is raised into a ring, and is crenate (*can. op.*, pl. 34, figs. 14, 15).

Specimens taken from decaying fish have very generally shown a marked diminution in both lateral frills and terminal rosette. Comparison of these with behavior of fresh specimens kept in culture media shows that the diminution is due to an actual disintegration of tissue. The lateral frills are cut off along a perfectly definite line, running in a slightly irregular antero-posterior course. The line can be made out some twenty-four hours before autotomy actually occurs. In every case where a specimen appears to have no lateral frills or noticeably reduced ones, examination shows a cut edge, along which the frills have dropped off. It is possible that Diesing's original figure was taken from a specimen in which this autotomy had taken place. The frills of the terminal rosette do not appear to be cut off in this regular fashion, but disintegrate on the margins only; ragged strings of tissue will be found attached to the body of the rosette. Most of the reduction in the size of the rosette in decayed specimens I believe to be due to intense contraction of that region, though undoubtedly accompanied by a certain amount of actual disintegration of tissue. When the parasite is left in the dead fish over twelve hours, at ordinary temperature, this decay begins.

The spines characteristic of this genus are very prominent in *G. fimbriata*. Their arrangement is in a constant pattern, characteristic of this species. This pattern is described in detail later, under the discussion of the cuticula, but its general outline will be given here also for the sake of convenience. In the anterior region, borne on the lateral "fins" above mentioned, are from five to seven rows of very large black spines (pl. 36, figs. 22, 23.) They are borne on very low papillae. There are about twenty-five of these spines; they vary in length, the more anterior and marginal ones being in general the larger. Their form and structure are discussed below, in connection with the description of the cuticula.

In the posterior region of the body, the spines are longer than those above described. They are borne on large rounded papillae. They form a "collar" (pl. 34, figs. 10, 12) around the region of the body between the funnel opening of the rosette and the canal opening. On the dorsal surface, no spines are found in front of this collar, which does not extend quite to the level of the canal

opening. On the ventral surface a line of scattered spines streams off laterally and anteriorly from the tips of this semi-circle to about the level of the receptaculum seminis. No spines are found on the lateral frills. The arrangement of the spines on the ventral surface (pl. 34, fig. 10) is a fairly constant one. It is of interest when considered in connection with Lönnberg's (1891) theory of the formation of the funnel and canal by means of the partial fusion of folds of the ventral body wall.

Gyrocotyle urna (Wagener) var.?

In the material collected by Dr. Kofoid near Monterey, off the California coast in 1904, were found three specimens differing from the rest in certain characters which seem to constitute a basis for specific distinction. Later, in 1907-1908, the writer found several similar specimens. The characters peculiar to this form are as follows:

1. The lateral frills are less voluminous.
 2. The folds of the posterior rosette are simple (*i.e.*, not thrown into irregular secondary frills, as in *G. fimbriata*), varying in diameter from one-sixth to one-third of the width of the body.
 3. The lateral frills do not extend to the base of the rosette but taper off gradually, disappearing posterior to the receptaculum seminis.
 4. Spines are present over the whole of the ventral surface as far forward as the middle of the length of the uterus, and extend thence in two lateral wings forward to a point just back of the level of the opening of the uterus. There is no distinct pattern discernible as in *G. fimbriata*. There are only a few scattered spines on the dorsal surface, except around the "collar," immediately in front of the base of the frill of the posterior rosette.
 5. The relative position of the opening of the penis, uterus, and vagina is markedly different from that seen in *G. fimbriata*. (See measurements, p. 381.)
- Except in two particulars, *i.e.*, the distribution of the spines and the fact that penis and vagina open at approximately the same antero-posterior level, this form seems to be identical with

Gyrocotyle urna as described by Wagener and Lönnberg. The distribution of spines may vary with age, though it has been found constant in specimens of all sizes of *G. fimbriata*. It is also possible that the non-appearance of the spines may be due to action of reagents on preserved material. The figure given by Wagener (1852) shows a very close approach to the pattern given above as characteristic for *G. fimbriata*. The whole question of distribution of spines cannot be settled until more material is available.

The question whether penis or vagina opens more anteriorly is a difficult one. In specimens killed between glass plates, these relations can be very easily distorted. On the other hand, in specimens not killed thus, it is very difficult to compare the positions of the two openings, as they are on opposite surfaces of a body too thick to be made transparent by clearing agents. The specimens in my possession show the two openings at practically the same level, with a small range of individual variation, depending upon the degree of extrusion of the penis-papilla.

Not having specimens of *G. urna* for comparison, it has been impossible to decide whether this form is really a distinct one, or belongs to Wagener's species. Until comparison can be made, it will be referred to as *G. urna* (var.?).

III. BEHAVIOR OF THE LIVING ANIMAL.

The shape of the body varies greatly in the living animal, and also in preserved specimens. Wagener's figures (pl. 48, figs. 84, 85) are the best in the literature, so far as giving a faithful reproduction of the appearance of the living worm. His figure of the preserved specimen, on the other hand, resembles very slightly any specimen that has come under the writer's notice. The acetabular extremity of the living animal is extended into a long, slender, cylindrical proboscis, along the sides of which the spines above referred to are distributed. This part of the worm is in constant motion. Posterior to the genital openings, in the region of the lateral frills, the body is flattened, slightly convex dorsally. Posterior to the uterus the lateral frills become less deep, and the body less flattened. This "neck" region can be very considerably extended. On the posterior extremity is borne the rosette, of

greater size in *G. fimbriata* than in *G. urna*, and its folds many times as complex, but generally held in a position exactly like that shown in Wagener's second figure, that is, the opening of the funnel, the rosette surface, lying, not at right angles to the surface of the body, but parallel to it.

The stage shown in Wagener's first figure represents the most extreme stage of expansion noted by the writer. No stages corresponding to those figured by Lönnberg (pl. 33, figs. 1-4) were seen, although the specimens observed were in many cases perfectly fresh and very active, contracting and expanding with great freedom, and moving about in the dish. But the shape of the posterior rosette was never materially altered, nor did the lateral folds completely disappear. Further, in the observations by Wagener, by Dr. Kofoid, and by the writer on the worm, an expanded condition always involves expansion of the acetabular extremity as well as the neck of the rosette. None of Lönnberg's figures shows anything suggesting the very characteristic acetabular extremity as first figured by Wagener. In observations of twenty-three living worms the writer has never failed to find the acetabular extremity assuming and maintaining this appearance throughout the period of activity. Lönnberg's observations, as above noted, are corroborated by Olsson (1896), who adds the astonishing statement that the worms preserve this form in alcohol. As the parasite is exceedingly sensitive to chemical stimuli, and invariably reacts to even a very dilute solution (5 per cent.) of alcohol by strong contraction, this seems to indicate that Olsson at least was dealing with some form other than *Gyrocotyle*. The writer found on two occasions, while searching for *Gyrocotyle* in *Chimaera colliei*, a distome strongly suggesting Lönnberg's figure and maintaining its shape in killing fluids, which might have been mistaken for *Gyrocotyle*. But since Lönnberg states explicitly that these transformations in form took place under his eyes, this explanation seems scarcely possible. We are forced to accept a discrepancy in results here, only to be removed by further investigation.

The living worm, in the intestine of a fish that has just been caught, is translucent, of a dull pink color, exactly similar to the intestine on which it lies. The worm in perfectly fresh fish

is firmly attached by the terminal rosette, which is spread over an area of ten to twelve millimeters in diameter. The folds of the rosette fit over the villi of the intestine. The canal opening (on the ventral surface) is closed as long as the rosette remains attached. A series of waves of contraction passes from the margin of the rosette toward the canal opening, during the attachment of the rosette. The lateral frills are present even in the most expanded state of the worm, constituting one-half of the total width of the body. The acetabulum is very active, thrusting itself backward, under, over or to the side of the body. The whole worm contracts and expands frequently without any apparent stimulus. The parasite is not easily affected by mechanical stimuli under these conditions, but will contract if exposed to direct sunlight, and is very sensitive to chemical stimuli. The acetabulum has never been found attached, or in any sense functioning as a sucker. This statement is borne out by all investigators.

Shortly after the death of the fish, the fluid intestinal contents become thick and opaque, and the worm detaches itself and contracts, losing its translucence and becoming creamy-white in color. The region of the mucous membrane to which the rosette has been attached is of a deep purplish red, and appears inflamed after the rosette has detached itself. Many of the worms are found in this opaque condition, and do not again become active. From observations on the behavior of the attached specimens, and from the fact that inactive specimens are found in all parts of the intestinal tract, in the mouth and on the gills, it appears fairly certain that the worm attempts to leave the dead host, and very frequently succeeds in doing so. In one case, the worm was found crawling up the first turn of the valve, when the intestine was opened. The fact that specimens are so often found, either in the first or next to the last turn of the valve, also points to this conclusion. Finally, the finding of a living specimen crawling on the bottom of a jar of sea-water in which a *Chimaera* had been placed, is fairly conclusive evidence that the worm occasionally succeeds in escaping from its host. The parasite is never found attached elsewhere than in the spiral valve. Spencer (1889, p. 138) remarks in this connection: "The specimens

[of *Gyrocoyle rugosa*] obtained by myself—three in number—were taken from the mouth of *Callorhynchus antarcticus*, and their presence in such a position was doubtless associated with the fact that the fish had been dead some twenty-four hours, though the parasites were still living and evidently trying to find their way out of the dead body.” Wagener (1852, p. 543) says: “Nur einmal fand es sich an den Kiemen, wobei jedoch bemerkt werden muss, dass die Fisch schon 12 Stunden ausserhalb des Wassers sich befand.” Lönnberg (1891) mentions the finding of *G. urna* living free, but supposes the worms to have finished their cycle and to have been cast out with the excrement of the host. He seems to imply in the following statement that the worms leave the dead host (writing of the almost invariable occurrence of the parasite in *Chimaera*): “In zwei anderen, die ich in Upsala untersuchte, die aber von Trondhjem stammten, habe ich ihn nicht gefunden, aber diese Fische waren schon seit mehreren Tagen ausserhalb des Wassers.” It may then be regarded as an established fact that the parasite is capable of a very considerable amount of locomotion, and that it can, under favorable conditions, leave its host and live for some days outside the intestinal tract. The most important condition seems to be temperature; a low temperature (about 10°-12° C.) is most favorable. In warm weather the worms remain active for only a very short time, and have never succeeded in getting out of the intestine in any case under my observation. This ability to leave the host, taken in connection with the behavior of the isolated parasite as described below, has an important bearing both on the problem of orientation and on the question of the habitat of the parasite, which will be discussed later.

The worms on being removed from the fish were placed in culture fluids. The worm is very active, if removed soon after the death of the fish and kept at a low temperature. The culture solution quickly becomes contaminated with bacteria, and the worm contracts and grows sluggish. When changed to fresh solution the parasite expands and renews its movements. These consist of the following:

1. Thrusting and exploring movements of the acetabular extremity, accompanied by contraction and expansion of the body.

2. "Righting-up" movements, in which the worm turns from one surface to the other. These take place when the worm is placed on its dorsal-surface and also when it is exposed to strong light.

3. This turning over is accomplished in two typical ways, either by turning completely over on one side on the frills as an axis, or by a more elaborate process of tucking under the acetabulum until it emerges posterior to the rosette, when the rosette is elevated and the overturning accomplished after the manner of a somersault.

4. A rotation from side to side of the terminal rosette, accompanied by a wave-motion in the margin of the frills, takes place during the worm's most active period.

5. Locomotion in a definite direction is accomplished by means of a series of expansions and contractions, with some help from the mobile lateral frills. The acetabular extremity is in every case directed anteriorly; the rosette is held in the typical position, raised, with the canal opening ventral and the funnel opening dorsal. The acetabulum is thrust out, and the whole body elongates, the rosette remaining stationary. This expansion leaves the rosette end where it was before, the acetabular end some two centimeters further toward the goal than at start. Then a wave of contraction sets in, bringing the rosette end nearer the acetabular end, which also moves backward a short distance, approaching the rosette. The net result is an advance in the acetabular direction. The acetabulum remains contracted, while the rest of the body expands. In this expansion the rosette must either retreat, or the whole contracted anterior extremity be shoved forward. The latter is what actually occurs, as shown by careful marking of the relative positions of the two ends before and after the wave of expansion. This method of procedure is very effective, resulting in an average gain of about two centimeters for each wave of contraction. A distance of fourteen centimeters was traveled in ten minutes by one specimen; but in this case more than the average gain was made, the whole distance being accomplished in five contractions.

IV. CHARACTERISTICS FOR SEPARATION OF SPECIES.

The characteristic peculiarities of each species have been set forth by its discoverer, but there has been no systematic attempt to assess the worth of these characteristics for the genus as a whole since that of Braun (1894). He was not acquainted with at least one very important set of species characteristics, that proposed by Haswell (1902).

The first species characteristics were proposed by Diesing (1859). He distinguishes *G. rugosa* from *G. urna* by the presence of lateral frills and spines and the greater size of the tail rosette in that species.

Monticelli also recognizes these two species, separating them by the following points:

1. The absence in *G. rugosa* of the frilled lateral margins.
2. The greater length of the uterus in *G. rugosa*, possibly correlated with the following character.
3. The presence of hooks in the embryo within the uterus of *G. rugosa*.

Braun (1894) recognized *G. urna* and *G. rugosa*, but only as doubtfully distinct. The basis for separation he finds in the position of the opening of the vagina and penis; the former being the more anterior in *G. urna*, the latter in *G. rugosa*.

Haswell (1902) recognized *G. urna* and *G. rugosa* and tentatively proposed a new species, *G. nigrosetosa*. He distinguished *G. rugosa* from *G. urna* on the following grounds:

1. Relative position of the apertures of penis and vagina.
2. Presence of an eversible cirrus adapted to self-impregnation in *G. rugosa*.
3. Spinules lining the ejaculatory duct in *G. urna*.
4. Presence of hexacanth embryo in the uterine egg of *G. rugosa*.
5. Shape of spines.

G. nigrosetosa he distinguishes on the following grounds:

1. Size of eggs, 0.08 mm., as distinct from eggs of *G. rugosa*, 0.1 mm.
2. Presence of operculum, distinct from *G. rugosa* and *G. urna*.

3. Absence of hooked embryos.

After careful comparison of the available figures and descriptions and a study of about forty specimens, ranging in state of preservation from those perfectly fresh, attached to the intestine of the host, down to badly disintegrated specimens from various regions of the alimentary tract of decomposing hosts, the writer has found certain of these proposed criteria to be useful and valid. Certain others seem untrustworthy. These specific characters may be listed and criticized as follows:

1. *Presence of lateral frills*.—It seems fairly certain that lateral frills are present in all species of the genus, when the specimen is in a good state of preservation. Presence of the frills is therefore not a basis for specific distinctions. The amplitude of the frills, and their relative width (in terms of total body width) for any given state of contraction or expansion, is however a characteristic of real value in the recognition of species. *G. rugosa* (pl. 38, fig. 36) has comparatively scanty and narrow frills; in *G. nigrosetosa* the frills are deeper and more voluminous; in *G. urna* (pl. 47, figs. 84, 85) they are twice the depth of those in *G. nigrosetosa* and many times as voluminous. In *G. fimbriata* (pl. 34, fig. 10) they are still more ample and about the same depth as in *G. urna*. While these differences can be easily seen, the extreme contractility of the animal makes it impracticable to attempt to use this characteristic as a basis for separation of species. It is a concomitant, rather than a critical characteristic, not available for exact description.

Diesing's specimen without frills was taken, it will be recalled, from *Mactra*. According to the best of our knowledge the only host of the adult parasite is some member of the family *Chimaeridae*; this specimen, having been set free from its host in some fashion, probably entered the shell of the mollusk by accident. Certainly not adapted to life as an ectoparasite, processes of disintegration would undoubtedly speedily set in, and my own experiments with *Gyrocoyle* in culture media show that deterioration invariably begins by cutting off of the lateral frills in increasingly deeper layers.

2. *Presence of spines*.—This is critical only when applied to living specimens and to those which have been preserved in such

a manner as not to injure the spines. In addition to the effect of reagents, disintegration results in the early loosening and disappearance of the spines. In no case where the living worm has been examined have the spines been absent.

The distribution of the spines affords a useful basis of distinction. In *G. rugosa* (Spencer, 1889), "spines are scattered over the whole surface of the body"; in *G. nigrosetosa* (Haswell, 1902) "they are mainly confined to the dorsal surface, except at the anterior end. Over the rest of the ventral surface are scattered a very few, much smaller than those on the dorsal surface." In *G. urna* (Lönnberg, 1891), the distribution is confined to the extremities and the lateral margins of the body, leaving the middle of the body, from just in front of the canal opening to the level of the acetabulum, free from spines. In *G. fimbriata* the condition is as described by Lönnberg for *G. urna*, except that spines are absent from the greater part of the lateral margin of the body, and do not occur on the lateral frills. Possible variation with age and the ease with which spines may be lost by slight disintegration or action of reagents, makes any distinction resting on them somewhat impracticable. Here again we have differences coördinated with, but scarcely useful as, specific distinctions.

3. *Size of tail rosette.*—This character appears to depend less on the state of contraction than do the width and amplitude of the lateral folds, and if reduced to a definite statement in terms of some other dimension of the animal, would probably be found to vary about a mean characteristic for each species. The astonishing illustrations given by Lönnberg (pl. 33, figs. 1-4) would, if corroborated, not necessarily invalidate the worth of this characteristic, provided comparisons were made between specimens in a similar state of contraction. *G. rugosa* (pl. 33, figs. 5, 6) in a contracted state has a rosette about one-fourth its greatest body-width in diameter. In *G. nigrosetosa*, the rosette is about five-sixths the body-width; in *G. urna* about one-half; while in *G. fimbriata* it varies from two-thirds to three-fourths or even more.

4. *Length of uterus.*—This is a character which it is exceedingly difficult to apply. The length of the much-contorted

uterus is hard to estimate, the number of turns may vary with the state of contraction, and certainly varies with age. I have been unable to reduce this to definite measurements. From Spencer's diagram it seems probable that the uterus occupies more space in *G. rugosa* than it does in *G. fimbriata*, or, according to Haswell, in *G. nigrosetosa*.

5. *Presence of hooked embryos in uterine eggs.*—This is a character easily applied and apparently thoroughly critical. It serves to set off *G. rugosa* from the rest of the genus.

6. *The relative positions of the openings of the penis and vagina.*—This character is perfectly definite and, applied to material not flattened under pressure when killed, seems trustworthy. There is one possible source of confusion, in the fact that the penis opening is on the summit of a papilla, very mobile and capable of considerable extension. The vagina is fixed in position. In case this papilla should be fully extended, the penis opening might lie in front of the vagina; while if withdrawn it would lie well behind it. The same criticism might hold for medio-lateral relations. The fact that *G. rugosa*, the only form in which the penis papilla has been observed greatly extruded, is also the only one in which the opening is definitely in front of the vaginal opening, suggested this possible source of error. Spencer's figure seems to point in this direction.

7. *Presence of an eversible cirrus, adapted to self-impregnation.*—This arrangement has been reported only by Haswell for *G. nigrosetosa*. It does not seem probable that only one species of the genus possesses a type of cirrus adapted to self-impregnation, especially when it is reflected that single individuals of all reported species have been found repeatedly in their hosts. It is strange that no eversion of the cirrus has ever been noted in any except the one specimen of *G. rugosa* studied by Haswell, and possibly in the one figured by Spencer.

8.—*Spinules lining ejaculatory duct.*—This character is of service in setting off *G. rugosa* from the rest of the genus; spinules (interpreted by Lönnberg as cilia) have been observed in the ejaculatory duct of *G. nigrosetosa* by Haswell, of *G. urna* by Lönnberg, and in *G. fimbriata* by the writer.

9. *Shape of spines.*—The data on this point need revision.

The shape of the spines may vary somewhat in different regions of the same animal. Furthermore, all the spines thus far described correspond exactly to those figured by Lönnberg, with the exception of Spencer's figure of the spines of *G. rugosa*. Possibly a study of more individuals of the latter species may show closer similarity to the type of the genus.

10. *Size of eggs.*—This character must be regarded with some distrust, in view of the fact that one individual may yield ripe eggs varying in size from 0.075 mm. to 0.115 mm.

11. *Presence of an operculum in the egg-shell.*—Haswell (1902) figures an egg of *G. nigrosetosa*, having a thick shell, with a thin plate at one pole, in diameter less than one-third the greatest transverse diameter of the egg (see my plate 47, figure 81.) "A circular area of the shell at one pole is much thinner than the rest, and is probably differentiated as an operculum." The same observer studied eggs of *G. rugosa*, and states that in them the shell does not appear to be provided with an operculum. The eggs of *G. fimbriata* show when discharged no such thin plate; but eggs taken from poorly preserved specimens show an operculum, its diameter a little more than half the greatest transverse diameter of the egg, in which the shell is slightly thinner than elsewhere. Its margin is serrated. This cap differs in size, thickness, and character of margin from the operculum of Haswell, but seems to be an homologous structure. The significant point is that there is no trace of it in the freshly discharged ova, and that it does appear very clearly later. Probably the ova of *G. urna* and *G. rugosa* would also show a similar structure, at a similar stage. The problem is whether Haswell's operculum is present in a freshly discharged or intra-uterine egg, or whether it is merely an early stage of the formation of this cap. Only in the former case does the operculum become a good specific character. Haswell explicitly observes that "the specimens were not in good condition for minute investigation." His figure (see my plate 47, figure 80) shows the neck of the rosette as swollen, recalling an appearance characteristic of worms kept too long in culture media. But in the absence of any definite statement as to the condition of the two specimens of *G. nigro-*

setosa, the presence of an operculum in uterine eggs must be adopted as a specific characteristic of *G. nigrosetosa*.

In addition to these characters which have been proposed and found trustworthy, the writer suggests the following:

1. *The character of the folds of the terminal rosette, whether simple or complex.* This is correlated with the greater relative size of the rosette; but the fact that the size varies greatly and is difficult to express in a ratio that could be applied to any specimen to be determined, makes the character of the folds themselves seem a more easily applicable test. The writer is convinced that this character is constant in all stages of contraction, at all ages, and after treatment with all the ordinary reagents. It becomes unrecognizable only after decay has proceeded very far indeed.

2. *The ratio between the distance from the opening of the uterus to the tip of the acetabulum, and the distance from the opening of the uterus to the level of the opening of the penis.* While these absolute distances vary enormously with the state of contraction, a series of measurements shows that the ratio is fairly constant about a mean characteristic of the species.

TABLE I.

Ratios of Measurements of Position of Genital Pores in *Gyrocotyle*.

<i>G. fimbriata</i>	<i>G. urna</i>	<i>G. rugosa</i>	<i>G. urna</i> (Wag.)	<i>G. nigrosetosa</i>
.4615	.266	.515	.333	.490
.4500	.222	.582		
.4444	.200	.592		
.4444	.200			
.4375				
.4375				
.4295				
.4295				
.4295				
.4290				
.4000				
.4000				
.3809				
.3333				
.3333				
.3333				

V. KEY TO SPECIES OF *GYROCOOTYLE*.

On the basis of the above discussion, the following classification is proposed:

A. Frills of posterior rosette simple.

- I. Uterine eggs containing hooked embryos. Opening of penis laterad of, and anterior to, vaginal opening.

G. rugosa.

Host: *Mactra edulis*. Diesing (1850, p. 408) Brazil. Monticelli (1889b, p. 228).

Callorhyncus antarcticus. Monticelli (1889c, p. 327), Dunedin, N. Z. Spencer (1889, p. 138), Australia.

- II. Uterine eggs not containing hooked embryos. Opening of penis mediad to vaginal opening.

- (1) Opening of penis posterior to vaginal opening.

(a) Eggs without operculum.

G. urna.

Host: *Chimaera monstrosa*. Wagener (1852, p. 545). Nice. Kröyer, Dänmark's Fiske, v. 3, p. 813. Van Beneden and Hesse (1864, p. 54). Olsson (1868, p. 58; 1896, p. 508). Lönnberg (1891, p. 14). Bergen, Christiania. Monticelli (1889b, p. 229; 1889b, p. 327). Mediterranean. Hansson. Free-living off the west coast of Sweden. (Lönnberg, 1891, p. 14).

(b) Eggs with operculum.

G. nigrosetosa.

Host: *Chimaera ogilbyi*, Haswell (1902, p. 48). Australia.

- (2) Opening of penis at the same level as vaginal opening.

G. urna (var?)

Host: *Chimaera colliei*, from the California coast. Has been found attached by terminal rosette to mucosa of spiral valve.

- B. Frills of posterior rosette complex. Opening of penis mediad to vaginal opening, at same level.

G. fimbriata.

Host: *Chimaera colliei*: off the California coast. Has been found attached as above, free in intestine, and in mouth and on gills of host.

D. GENERAL MORPHOLOGY AND HISTOLOGY OF GYROCOTYLE.

I. MATERIAL AND METHODS.

The structure of the worm has been studied in living specimens, in whole mounts stained and cleared, and in serial sections. The following killing fluids were used: Gilson's fluid, acetosublimate, Zenker's fluid and Vom Rath's mixture. The greatest difficulty is found in preventing extreme contraction of the specimens. Stupefaction with chlorethane resulted in contraction as intense as that produced by the killing fluid: the use of hot reagents was of some small advantage. Flattening between plates of glass gave the least contraction, but had the disadvantage of producing some distortion. The best results were obtained from specimens killed in Zenker's fluid; the poorest from those killed in Gilson's fluid. It is difficult to obtain good infiltration with paraffine, especially in the normal (not flattened) specimens. The modification of Apathy's method given by Lee was very successful, leaving the tissues in good condition. High temperatures (over 50° C.) are rapidly fatal to the integrity of the tissues. The shortest possible time in paraffine of the lowest melting point that can be used gives the most satisfactory result.

The worm is very difficult to section because of the great mass of eggs it contains. Various macerating agents were tried, but none was of any great service. Sections were cut as thin as 4μ ; most of the series ranged from 8μ to 16μ , the latter in collodion.

The stains used were: Heidenhain's iron haematoxylin, Benda's iron haematoxylin, Mayer's acid haemalum, Mallory's connective tissue stain, Delafield's haematoxylin, Ehrlich's haematoxylin, Lönnberg's borax carmine-Lyons blue, toluidin blue. Iron haematoxylin preparations are excellent for the study of cuticula, musculature and sex-cells; they are worthless for the study of the nervous system and unreliable in many details. No statements are based on results given by this stain alone.

Mallory's connective tissue stain colored nervous tissue, with the exception of the nuclei, bright blue. Its action was too

uneven to be of special value. Mayer's acid haemalum, Delafield's haematoxylin and Ehrlich's haematoxylin gave satisfactory results for general morphology. Lönnberg's borax carmine-Lyon's blue method gave the best result for the study of the nervous system. This in general is the method used by Lönnberg in his work on *Gyrocotyle*. A brief description of the process is given by him (Lönnberg, 1891). The material is stained *in toto* in Grenacher's aleoholic borax carmine, 60% alcohol, decolorized in acid alcohol (5 drops conc. HCl to 100 cc.); after sectioning and mounting the sections are run very quickly through absolute and 90% alcohol to a saturated solution of Lyon's blue in 60% alcohol, plus three drops n/10 HCl to 35 cc. of stain, where they remain fifteen minutes. The sections are decolorized in ammoniacal 85% alcohol made up of one part 85% just basic to litmus to 4 parts neutral 85%. Decolorization requires from two to three minutes and must be stopped when the sections appear violet in color. On washing in neutral 90% the differentiation takes place. The sections must not be left in 90% or absolute longer than one or two seconds, else the stain is blurred. This method gives beautiful preparations in so far as differentiation of tissues is concerned, but is rather poor for cytological differentiation, especially in cell-boundaries.

The nervous system stains uniformly a light blue, easily distinguished from all other tissues except condensed connective tissue. The blue is clearer in the nerves than in the connective tissue; the nervous tissue can easily be recognized with a fair degree of certainty by this fact, coupled with its distinctive histological structure.

The statement generally made that Lyon's blue should be used in very dilute solution for corrosive sublimate material is not applicable in this case. Weak solutions give no result, for all the color drops out at once, leaving no differentiation.

II. BODY-COVERING AND SPINES.

The body is covered by a thin membrane, composed of finely felted fibres imbedded in a homogeneous matrix (*cut.*, pl. 42, figs. 55, 58). These fibres are exceedingly delicate, tangled in an irregular fashion, but in general parallel to the surface of the

body. The outer surface of the membrane is bounded by a fine, deeply stained layer of ragged fibres (*ext. cut. l.*). This is seen only in perfectly preserved specimens. Vesicles occur frequently in the membrane. There are also breaks in the margin, resembling sections of the "pore-canals" figured by Blochmann (1896). The thickness of this membrane varies in different regions, being slightly less on the lateral folds and on the surface of the acetabulum. The average thickness on the surface of the body proper is about 3.8μ ; on the lateral folds, etc., about 2μ . This membrane will be referred to as a "cuticula," following the common usage among writers on the subject; but the word is not used in its strict sense, as denoting a body-covering derived from an underlying epidermis. The cuticula of *Gyrocoyle* may or may not be derived from the "subcuticular" layer referred to below; structural relations indicate that it is, but in the opinion of the writer the question can only be settled by embryological data which are not available.

Lönnberg (1891) describes a two-layered cuticula, agreeing in general with the appearance of that of *G. fimbriata*; but he describes the fibres seen in the "Hauptschichte" or principal layer, as running perpendicular to the surface. He finds this only in sections in which the cuticula is torn or affected by reagents; from appearances presented in similar sections, the writer thinks he was probably dealing, not with the cuticular layer, but with a layer of perpendicular fibres lying beneath the cuticular muscles, to be described later.

Immediately beneath the cuticula (*cut. trans.*, pl. 42, fig. 55) is a layer of cuticular muscle-fibres running round the body at right angles to its long axis (*cut. trans.*, pl. 42, fig. 58). Close beneath this layer lies a set of longitudinally arranged muscle-fibres (*cut. long.*); these are heavier than the transverse fibres. These layers of muscles are distinguished as the cuticular musculature. Some distance below these muscle fibres is an irregular layer of large nuclei, about twice the size of the ordinary parenchyma nucleus, resting on and often imbedded in the outer transverse layer of body musculature (*sub. cut.*). This layer may be one or two nuclei deep, or it may be from five to eight deep. In the neighborhood of a spine the layer becomes three

to five times its ordinary depth. These nuclei, the "Matrixzellen" of Lönnberg, are richly supplied with chromatin. Definite cell-boundaries can sometimes be seen; the cytoplasm stains deeply and shows a granular structure. The writer was unable to establish any processes running from these cells out to the cuticula through the cuticular muscle-fibres, or to make out any structural connection existing between cuticula and subcuticula. The space between the subcuticular layer and the longitudinal cuticular muscles is filled with very delicate muscle-fibres (*sag. fib.*) and thread-like processes of the subcuticular cells, taking in general a direction perpendicular to the surface. There are also many fibres running parallel to the surface, as shown in transverse section by their cut ends, but these are not so conspicuous as the perpendicular threads. It was probably this layer which Lönnberg mistook for the principal layer of the cuticula in his sections. The writer has found similar appearances, due to the fact that the cuticula is very easily affected by reagents. In a specimen preserved in early stages of decomposition or imperfectly fixed by the killing fluid, the cuticula is almost invariably found to be sloughing off in thin strips, broken, notched and ragged. It presents both horizontal and perpendicular planes of cleavage, but shows a marked tendency to split in layers parallel to the body-surface. This is the only indication of lamination noticed; it is more justly interpreted as a splitting in the direction taken by the greater portion of the fibres of which it is composed.

The cuticula in the region of the rosette shows marked changes. That lining the funnel is noticeably thinner, the cuticular muscular layers are much reduced, and the subcuticular cells are very few. As the much-folded margin of the funnel is approached, the subcuticular cells of the outer wall also become much reduced, sink deeper and cease to be a distinct layer; lying within them large gland cells can be seen. In the writer's opinion these are not related to the subcuticular cells but belong to the central part of the body just as do the shell-glands and the prostate glands, arising in the neighborhood of the inner longitudinal muscular layer.

The most prominent feature of the body-covering is the

spines, frequently referred to in the preceding discussion of the literature of the subject. In *G. fimbriata*, the spines are arranged in a definite pattern, from which there is no great amount of individual variation, though the number of spines varies considerably. At the anterior extremity, on the lateral fin on each side of the acetabulum are two groups of large spines (pl. 36, figs. 22, 23). They are arranged in five rows, two each on the dorsal and ventral surfaces and one row on the margin. There are from five to seven spines in a row, from 20 to 30 in each group. Here, as elsewhere, the spines are borne on rounded papillae, which are in this region of greater size than elsewhere on the body, except around the "neck" of the rosette. The papillae extend back along the lateral fin to the beginning of the lateral folds, but bear spines only at the region shown in the figure, at the level of the posterior half of the acetabulum. In addition to these large spines, of the shape shown in fig. 28, there are a number of very much smaller, less definitely shaped spines (pl. 37, fig. 32), in among the larger ones.

There are no spines on either surface, throughout the length of the body, back to the posterior border of the receptaculum seminis. Here on the ventral surface two groups of spines appear, near the base of the lateral folds, extending backward in converging lines toward the canal opening. They flank this opening, increasing in number and size, and spread out posteriorly on the surface of the neck of the rosette in its median half. At the posterior border of the neck they extend laterally, passing around to the dorsal surface. On the extreme lateral margins of the ventral surface appear two groups of spines, which pass over on the dorsal surface, forming with the ring above described a belt of spines on the dorsal surface of the neck. The number and direction of these spines is shown in the figures (pl. 34, figs. 10, 12).

In *G. urna* (var.?) the distribution of spines (pl. 36, fig. 24; pl. 34, figs. 11, 13) is markedly different. The ventral surface, to the level of the uterus opening, is thickly set with large spines; there is no special pattern in the arrangement about the neck, there being six or seven irregular rows of spines, encircling the base of the rosette. On the dorsal surface the spines are

fewer and scattered irregularly over the whole surface. It should be noted that the two marginal clumps of spines at the level of the acetabulum occur as they do in *G. fimbriata*.

The distribution of spines was worked out in living as well as preserved material, that no error due to loss of spines by deterioration or action of reagents might enter. The distribution found resembles that given by Lönnberg for *G. urna*, except that he describes spines as present along the whole length of the lateral margins of the body, and along the lateral folds. The distribution as given by Spencer (1889, p. 140) for *G. rugosa* is substantially that found in *G. urna* (var.?) :

"They are distributed generally over the body surface, but are most numerous along the side folds, and more especially at the anterior end, both on the dorsal and ventral surfaces, and again at the posterior end, beyond the region of the side folds. They are sparsely distributed over the central part of the body, both dorsally and ventrally."

Haswell's figures (see my plate 47, figure 80) show spines of great size distributed over the whole of the surface of the animal. Wagener's (1852) figures show the acetabular clumps, and a distribution of the spines in the posterior region similar to that described by Lönnberg and given above for *G. fimbriata*.

The small spines, irregularly distributed, vary in size from 40μ to 60μ by 15μ to 25μ , and in shape from simple rounded spinules to a blunt-tipped, swollen-based form. Broad, triangular, sharply pointed forms also occur, but less frequently (pl. 37, fig. 32). These spinules are not borne on papillae; they rarely contain more than three concentric layers.

The spines proper, from the extremities of the body, are of fairly constant shape and size. In the acetabular region (pl. 37, figs. 28, 29) they are bluntly rounded at the tip, swollen in the middle third of their length to nearly three times the diameter of the tip, narrowing again at the bluntly rounded base. They are about 130μ by 36μ in size. In the rosette region, the spines are of the same general shape (pl. 37, figs. 30, 35), but are of considerably greater size, ranging from 185μ by 45μ to 220μ by 55μ .

The spines are composed of concentric layers of uniform thickness, and are hollow. In macerated specimens the layers

are seen to be composed of a finely felted mass of fibres, circular in general direction, embedded in a homogeneous interstitial substance which is acted on by the macerating agent (which also removes the cuticula from the body) (pl. 37, fig. 33). Each spine is set in a pit lined with a very thin cuticula of felted fibres (*parafelt*, pl. 37, fig. 34) which passes indistinguishably into the fibres of the surrounding parenchyma. The spine is surrounded by muscle-bundles, which serve to protrude and retract the spine. The retractors are muscle-bundles from the outer transverse layer of the body musculature; they insert at the base of the spine (pl. 37, fig. 30). The protractors are bundles of fibres inserted at the base and for some distance on the sides of the spine; they originate or are attached to the cuticular musculature, principally to its transverse layer.

The direction of the spines is shown in the figures (pl. 34, figs. 10-13). In general they may be said to be directed anteriorly and laterally. This is the most advantageous arrangement possible for maintaining the attachment of the parasite to its host; the position of the greatest number of spines on the ventral surface and around the rosette also further this end. For locomotion, the spines seem to be arranged to hinder rather than help; but they are probably so completely retracted that their rounded ends offer no special resistance to the forward movements of the worm. At all events, however theoretically difficult their arrangement and direction render locomotion, the worm does move, and with considerable rapidity, in spite of them. Naturally, ease of locomotion is a secondary and firmness of attachment a primary consideration in the economy of this creature.

III. MUSCULATURE.

The musculature of *Gyrocotyle* is exceedingly well developed, and composed of powerful, neatly balanced sets of muscles. It constitutes the great bulk of the body. This is not surprising, when the extreme contractility and general activity of the worm is considered.

In general, muscles are grouped in pairs running at right angles to each other. There is throughout the body, but especially prominent in the region between the acetabulum and the

canal opening, a set of sagittal fibres, very delicate, not organized into bundles, running from the outer cuticular muscle layer of the dorsal surface to that of the ventral surface. The fibres insert directly in the cuticula, as do those of the protractors of the spines.

In addition to these sagittal fibres, six distinct coats of muscle fibres can be distinguished, in the body proper. These may be grouped according to their action, which gives us three sets of opposing muscles, each set a longitudinal opposed to a transverse; or they may be grouped according to their position with respect to the other tissues of the body. Such a division gives us two groups, one of which may be again subdivided into two.

1. *Peripheral*, including all muscles lying without the vitellaria. May be divided into:

- (a) Cuticular, including all muscles lying without the subcuticula or "Matrix-zellen."
- (b) Intermediate, including all muscles lying between the subcuticula and the vitellaria.

2. *Central*, muscles lying within the vitellaria.

The cuticular muscles have been described in connection with the cuticula (p. 385). Immediately beneath the subcuticular cells, frequently invading their territory, is a layer of muscle-bundles directed around the body, at an angle of about 60° to its main axis. Thus in a cross-section we get only broken segments of this layer, not a continuous sheet, as in the deeper-lying transverse muscle layer. These fibres run in two interlacing sets whose directions are at an angle of 60° to each other. These bundles all break through the subcuticula to insert by fine threads on the cuticula (pl. 42, fig. 55).

Immediately beneath the outer transverse layer above described are found the bundles of fibres running parallel to the longitudinal axis of the body. These are heavier and grouped into more definite bundles than any previously described. The layer is one or two bundles thick and occurs over the whole body, but becomes very thin in the region of the lateral folds. These fibres insert on the cuticular musculature, and with the outer transverse just described produce the transverse ridges so characteristic of the worm in its contracted state. Within this layer

lie the inner transverse muscles, a very heavy sheet of fibres running at right angles to the longitudinal axis, around the body. These fibres also are continued for some distance into the region of the lateral folds, but are considerably reduced. These muscle layers constitute the peripheral musculature and are found throughout the whole body, though less and less strongly developed the further laterad they pass.

Within the inner transverse muscles lie the vitellaria, the large excretory canals, the central nervous system, the glands of the reproductive system, and the strongest muscles of the body, the inner longitudinal. In the region of the body anterior to the testes and posterior to the ovaries, these muscle-bundles occupy the whole of the space inside the vitellaria. In the intermediate region, especially in the region of the uterus, the layer is considerably reduced, and pushed to one side. It is quite thick ventrally, but there are very few fibres dorsal to the uterus. These longitudinal fibres insert on the acetabulum, and around the neck of the rosette and on the walls of the canal. It is by the contraction of these powerful muscles that the worm moves about, thrusts forth and around and withdraws the proboscis-like acetabulum, and firmly attaches the posterior rosette. Furthermore, as Lönnberg pointed out, this muscle layer being absent in the lateral frills, and the outer longitudinal fibres being very weakly developed there, on contraction of the longitudinal muscles the lateral folds are increased in amplitude. Lönnberg regards the frills as due wholly to contraction of the body musculature; the writer, in agreement with Wagener, regards them as independent structures, existing in all states of expansion of the animal.

The musculature of the acetabular region (pl. 40, fig. 43) shows plainly the origin of the acetabulum as an invagination of the anterior extremity of the body. There is a doubling of the layers, giving twelve instead of six. By inverting the anterior extremity we get a mass of predominantly longitudinal muscles, corresponding to the inner longitudinal body-layer, on the outside of the acetabulum. These fibres are meridional with reference to the acetabulum as a whole and constitute more than half its bulk. Inserting along the surface of this mass are the inner

longitudinal muscles of the body, most numerous toward the anterior extremity and in large masses around the margin of invagination; on contraction of the inner longitudinal muscles, the whole mass of the acetabulum is drawn back (pl. 40, fig. 43). This is the state invariably found in killed specimens. In the living animal in the expanded state the mouth of the acetabulum is at the anterior extremity (pl. 33, figs. 7, 9); further evagination is impossible. The great lengthening of this region observed in active specimens must be due to expansion of the acetabulum itself.

The fibres of the outermost layer (*out. mer.*), constituting the bulk of the acetabulum, are derived from the inner longitudinal layer of the body and are meridional in direction, presenting in section a margin of cut edges surrounding the acetabulum. This layer is densely supplied with finer radial fibres (*rad. fib.*), at right angles to the long axis of the acetabulum, passing from dorsal to ventral surface. These are the homologues of the sagittal fibres of the body musculature, greatly increased in size.

Immediately within this outer heavy layer lies a set of fibres predominantly transverse (*out. circ.*), passing from left to right of the acetabulum, the homologue of the inner transverse layer of the body. This layer is even more abundantly supplied with radial fibres than is the outermost one. These pass from dorsal to ventral, at right angles to the radial fibres of the outer layer. Within this layer is a second set of meridional fibres (*in. mer.*); the homologues of the outer longitudinal muscles of the body, followed by a thin layer of fibres passing circularly around the opening of the acetabulum, corresponding to the outer transverse muscles of the body. Lying next to the cuticula are thin longitudinal and transverse layers, the homologues of the cuticular musculature elsewhere. At the mouth of the acetabulum a special sphincter muscle has been developed, composed of fibres from the inner transverse, the inner longitudinal and the circular muscle layers of the acetabulum (*acet. sphinc.*). Most of the fibres are circular in direction; they are grouped in heavy bundles and form a large ring-muscle about the acetabular opening.

The musculature of the funnel-region has been worked out

by Lönnberg (1891). There is here a doubling of layers, due to folding on the ventral surface, and an increase in the inner transverse layer to produce two "wing-muscles." Lönnberg's tabulation of the funnel muscles and their homologues in *Gyrocoyle urna* the writer finds substantially correct for *G. fimbriata*. Here as in the acetabulum the development has been mainly in the inner transverse layer, and in the sagittal fibres. By means of these a very effective sphincter is produced at the base of the rosette. Posterior to the collar or "neck" (the region occupied by this sphincter) and anterior to it near the canal opening, the development of the transverse muscle layer is much reduced, though still greater than in the body in general.

Lönnberg concludes from the above described arrangement of muscle layers that the rosette and canal were formed by a folding from the posterior extremity forward in the ventral surface. This was first a furrow or trough, which functioned as a sucker, a condition common among the lower cestodes; later the ventral walls fused to form a tube, and finally only the most posterior part of the tube functioned as an organ of attachment, its anterior extremity remaining open as the present ventral opening of the canal. Lönnberg hazards no opinion as to the significance of this anterior canal opening. Observations on the attached worm show that the mouth of the opening is always closed while the rosette is attached to the mucosa. When the canal mouth opens, flaring out as in Spencer's figure 2, the hold of the rosette loosens and the worm drops from the mucosa. During attachment there is a series of waves of contraction, running from the margin of the rosette forward to the canal opening. The whole posterior extremity thus forms a suction-cup of high efficiency. The musculature of the ventral canal-opening, developed from the peripheral muscles, is shown in plate 40, figure 44.

The finer structure of the muscles in *Gyrocoyle* is very simple. The sagittal fibres (radial fibres of acetabulum and rosette collar) are not aggregated into bundles but are simple strands running through the body, distinguished from parenchymal fibres by their size and also by the position of the nucleus (pl. 42, fig. 57). This lies to one side of the fibre, forming a

bulging prominence. These nuclei are larger and more easily seen than those of the other muscle fibres; this is in harmony with the generally primitive and undifferentiated character of this set of muscle fibres. In the outer transverse muscle layer the fibres are longer, very slightly swollen in the middle of their length, where the nucleus lies very closely applied to one side of the fibre. The nucleus also is elongated, rather than round as in the dorso-ventral fibre (pl. 42, fig. 57). In the two inner layers, the inner circular and the inner longitudinal, the nucleus is very hard to distinguish (pl. 42, fig. 56). The fibres are heavy, elongated, tapering gradually toward their extremities. The nucleus is exceedingly slender, flattened against the surface at one side of the fibre, but still within the fibre. In cross-sections of fibres the nucleus is difficult to distinguish, appearing merely as a thickening of the cell-wall; in longitudinal sections it can be made out more easily. Had not the nucleus appeared so unmistakably in the outer and sagittal muscles, it probably would have been overlooked in these inner fibres.

In the cuticular muscle fibres there is no trace of a nucleus. The fibres are slender, long, of even diameter. Those of the transverse layer are exceedingly fine, while the longitudinal ones are of ordinary diameter. The great number of processes running from the subcuticular cells, apparently to insert in the cuticular musculature, suggests most strongly that some of these cells, at least, are the myoblasts of the cuticular musculature. The fact that elsewhere in the body the nucleus lies in the fibre makes this seem improbable, yet the writer is at a loss to explain the processes and their connection with the musculature in any other way.

All the fibre bundles are penetrated throughout and enwrapped by parenchymal threads, with their accompanying nuclei. The latter can always be distinguished from muscle-nuclei by their shape and size, as well as by position.

It is of interest to note that Salensky (1874) found in *Amphiliina foliacea* smooth muscle fibres with laterally attached myoblast, this being one of the earliest cases in which a nucleus for a muscle fibre was discovered. Furthermore, the description above given of laterally attached nucleus in the dorso-ventral,

transverse and longitudinal muscles and of nucleus some distance removed from the fibre in the subcuticular muscles, corresponds to the classification given by Braun (1901, p. 1351). The only difference is that the laterally attached nucleus in *Gyrocotyle* is inside the fibre, not in an adjacent myoblast. The occurrence of nuclei within muscle fibres is reported, according to Braun (1894, p. 1351) in the scolex of the Tetrarhyncha, and in the longitudinal muscles of the proglottides of *Taenia dendritica*. That a form as primitive as *Gyrocotyle* should exhibit a muscle fibre relatively simple and undifferentiated as compared with that of the merozoic cestodes, is exactly what other facts in its structure would lead one to expect.

The staining reactions of the muscle-fibres are of some interest. With iron hematoxylin and toluidin blue the whole fibre stains very intensely. Preparations by these methods are excellent morphologically, mapping out the muscles most sharply; but are quite worthless histologically. With Mallory's connective tissue stain, muscle fibres stain a bright red. As nuclei also stain red, this method is not useful for a study of muscle-nuclei. The same holds true for borax carmine-Lyon's blue preparations. The best results are given by Delafield's hematoxylin, hematoxylin-eosin, or Mayer's acid haemalum, and counter-stains. With these the muscle-fibre stains a dull blue-gray, while the nucleus comes out sharply in blue-black.

IV. REPRODUCTIVE ORGANS.

The organs of *Gyrocotyle* include the following:

1. Female. Ovaries, receptaculum ovarum, vitellaria, shell-glands, uterus, vagina, and receptaculum seminis.
2. Male. Testes, vasa efferentia, vesicula seminalis, vas deferens, penis, and prostate glands.

All of these organs, with the exception of the vitellaria, lie within the inner longitudinal muscles. The female organs are in the second and third quarters of the length of the body; the male organs in the first quarter.

The ovaries (*ovar.*, pl. 39, fig. 42) lie laterad of the uterus, at its posterior border. They are roughly triangular in shape, the lateral lobes united in the median line just posterior to the

receptaculum seminis by a small median portion. They are composed of numerous rounded follicles, from which run collecting tubules to empty into five main oviducts, one posterior, two lateral and two anterior ducts. These lead into the receptaculum ovorum, which is embedded in a mass of loose tissue in a depression on the anterior dorsal surface of the receptaculum seminis. The receptaculum ovorum (*rec. ov.*, pl. 45, figs. 73, 75), is about 3 mm. in its antero-posterior and its dorso-ventral diameter and about 6 mm. in transdiameter. These measurements are the average for several sexually mature worms.

The *vitellaria* are composed of loosely-grouped follicles, each containing ten or fifteen cells, lying just within the inner transverse musculature and outside the inner longitudinal. The follicles are present throughout the body with the following exceptions: (1) dorsal and ventral to the uterus, that is, in the median third of the body in the two middle quarters or more of its length; (2) anterior to the posterior border of the acetabulum; (3) posterior to the level of the ventral canal opening.

The lateral folds are densely supplied with vitellarian follicles, these forming the greater part of the folds. The ducts of these yolk glands unite into four main lateral ducts, which empty into a yolk reservoir, or "Endstück," which lies in the dorsal depression of the receptaculum seminis above mentioned, just posterior to the receptaculum ovorum. It gives off a single efferent vitellary duct, which enters the afferent oviduct, as described below, a short distance back of the entrance of the duct connecting the efferent oviduct with the receptaculum seminis.

The *efferent yolk-ducts* (pl. 39, fig. 42, *vit. d.*), appear in stained and cleared preparations as a dark brown anastomosing network of delicate threads, spread over the receptaculum seminis and the first three or four coils of the uterus, and converging to the yolk-reservoir in the concavity of the receptaculum.

From the ventral surface of the receptaculum ovorum is given off in the median line a single *efferent duct* (*ef. ovd.*) which receives first a short thick-walled duct from the receptaculum seminis (*duct. sem.*); and then an efferent duct from the yolk reservoir (*ef. vit. d.*, pl. 45, figs. 71-74). This duct

(oot.) then becomes the uterus, passing to the left of the receptaculum seminis and around it to the ventral surface, across the ventral surface and forward, at once increasing in size. The first two or three coils of the uterus, as above described, may be regarded as an oötype. They are surrounded by shell-glands, and within them the compound eggs are formed. In the dorsal (proximal) part of the first coil, and to the left of the receptaculum seminis, the yolk-cells are seen to be aggregating about a single ovum and the uterus is full of droplets of a yellow homogeneous material, which form a coating around the combined ovum and yolk-cells. The uterus contains fully formed eggs in the convolutions anterior to the receptaculum seminis. It winds back and forth across the median third of the body through from fifteen to twenty convolutions, the duct increasing steadily in size, ending finally in a greatly dilated pouch which opens to the exterior by a large aperture on the dorsal surface in the median line posterior to the opening of penis and vagina.

The *uterus* is lined at its inception and throughout its course by a thin fibrillated layer, increasing in thickness from the posterior coils forward. This layer is covered with fine cilia, in the first five or six coils of the uterus. These cilia are connected with scattered nuclei beneath the cuticula, by means of delicate fibrils strongly suggesting those figured by Lönnberg (1891) for the cilia lining the excretory canals. Their direction is in general at right angles to the course of the uterus. These fibres lie in a nucleated meshwork of parenchymal fibres, which pass indistinguishably into the cuticular lining of the duct. Further forward, the nucleated circular muscle fibres disappear, and a typical subcuticular layer of cells appears coincidently with the appearance of a typical cuticular musculature, suggesting very strongly a structural connection between subcuticular and cuticular musculature.

The *shell-glands* (*sh. gl.*, pl. 39, fig. 42) are an aggregation of large cells, with characteristic nuclei, lying close to the receptaculum seminis on its dorsal, ventral, and posterior surfaces. This relation to the receptaculum seminis is of course due to the fact that the earliest convolutions of the uterus lie on these surfaces of the receptaculum. The greatest mass of cells lies to the

right and left; the posterior median mass is very thin. The lateral masses extend dorsally and ventrally well into the main longitudinal muscle mass, and in general the dorsal mass is greater than the ventral. The efferent oviducts and yolk-duets pass through this mass of gland cells, but no shell-material is seen except in the first coils of the uterus. The cells of the gland are large, swollen at the base, with slender "necks," leading into intracellular ducts (pl. 44, fig. 68). These ducts appear to open independently in the anterior wall. The cytoplasm of the gland cells is dense, granular, and stains very intensely. The cell wall is sharply defined. The nucleus is large, cloudy, with deeply staining border and faint nucleolus. The nucleus lies in the dilated base of the cell. The ducts have a sharply defined lumen, and are of considerable size.

The *receptaculum seminis*, originally described by Wagener (1852) as the testis, is a large chamber, convex posteriorly, slightly concave dorso-anteriorly, filled with a dense mass of semen (*rec. sem.*, pl. 39, fig. 42). It might be regarded as the dilated blind end of the vagina, which enters its dorsal surface near the anterior border. The receptaculum seminis measures about 1.5 mm. by 1 mm. by 1 mm. It is surrounded, as above noted, by the first coils of the uterus and their accompanying shell-glands; on its dorsal surface lie the yolk reservoirs, the receptaculum ovorum, and their efferent and afferent ducts. From the dorsal surface of the receptaculum is given off a short, thick-walled duct, the ductus seminalis, to the efferent oviduct.

The wall of the receptaculum seminis (pl. 42, fig. 59) is composed of a mass of finely felted fibres, elongated cells with large nuclei and granular, non-fibrillated cytoplasm. Outside this layer are found scattered cells of the shell-glands. This differs markedly from Lönnberg's description (1891, p. 41) of the histology of the wall of the receptaculum. "Das Receptaculum ist von einen dünnen Pflasterepithel ausgekleidet, aber es besitzt eine dicke fibröse Wand, die reich an eingeschalteten Kernen ist." The writer cannot distinguish cell walls in the lining of the receptaculum, but finds scattered nuclei, embedded in a mass of delicate interlacing fibres.

The receptaculum seminis contains, embedded in the mass of

spermatozoa, occasional deeply staining cells, large, and with very large nuclei. These were noted and figured by Spencer (1889, p. 146) : he suggests that they "may be simply the spermblastophores from which the ripe sperm have separated, but there is no proof of this." The writer is convinced that they are ova, which have entered the receptaculum seminis through the duct which leads from this structure to the oviduct, the ductus seminalis. The finding of these cells at the entrance of this duct into the receptaculum and their resemblance to the ova, renders this certain.

The passage to the oviduct, the ductus seminalis, has a very thick muscular wall lined with cilia and an exceedingly small lumen, often completely obliterated in sections. For this reason, Spencer was unable to demonstrate it to his own satisfaction, though convinced that it must exist.

The *vagina* passes forward, in the early part of its course much convoluted and lying close to the receptaculum seminis. Further forward it lies in the parenchyma close to the dorsal wall of the uterus; it turns ventrally near the middle of its course and passes gradually to the ventral surface, where it finally opens, laterally and posteriorly to the penis, near the right margin of the body. The lumen of the vagina is lined with a layer similar to that described for the receptaculum seminis, not ciliated. It is not epithelial, as described by Lönnberg. Its wall is composed of a thin layer of longitudinal muscle fibres; it is embedded in parenchyma and lies within the main mass of longitudinal muscles, close to the wall of the uterus. As the vagina nears the anterior margin of the uterus its lumen increases in diameter. During its course past the convolutions of the vas deferens this increase continues, and its wall is also increased in thickness. The lining of the tube becomes much convoluted in its course toward the left margin, and increases suddenly in diameter in the latter half of its transverse course, opening finally by a large aperture with much-folded margins and heavy muscular wall. This region is plainly adapted to copulation.

The *testes* are arranged in two groups not connected and not symmetrical (pl. 39, fig. 42). The left testis extends from the posterior border of the anterior third of the body, forward to

the opening of the penis. The right testis is composed of two lobes, the right and larger of which extends from the posterior level of the left testis forward to the anterior extremity of the body. The left lobe, attached by a narrow bridge posterior to the base of the acetabulum, lies to the left of the acetabulum and in front of the vaginal opening. The testes lie within the longitudinal muscle mass, in a position identical with that occupied by the ovaries in the posterior portion of the body. They are considerably larger than the ovaries, as is shown in plate 39, figure 42, and are composed of loosely-aggregated follicles. Each follicle is covered with a fibrous nucleated layer, the "tunica propria" of Lönnberg, continuous with the walls of the tubules into which the follicle opens. These unite into two main vasa efferentia and empty into a large median vesicula seminalis situated immediately in front of the uterus, nearest the ventral surface. This structure is perhaps more accurately described as a vas deferens, more or less uniformly dilated by the masses of spermatozoa. It coils from left to right and from dorsal to ventral, in three large convolutions (pl. 41, fig. 46), dilating near its anterior extremity to form a bulb, and opening through a muscular papilla into a thick-walled tube, the cirrus-pouch or ejaculatory duct. The wall of this pouch is thick and well supplied with muscles. Its inner lining is greatly folded and covered with delicate spinules. This duct passes almost straight dorsad, turning a little to the left, opening on a rounded papilla on the dorsal surface, a little to the left of the median line and anterior to the mouth of the vagina on the ventral surface. The wall of the duct grows much thinner toward its distal end and its lumen increases somewhat. Heavy bundles of muscle fibres running at right angles to the course of the ejaculatory duct are attached to its wall throughout the whole of its course (*rad. muse. f.*, pl. 43, fig. 65). Outside these lies a large mass of gland-cells extending the whole length of the ejaculatory duct. They are very large granular cells, with definite cell-walls forming intracellular canals (*prost. gl.*, pl. 43, fig. 64). These empty into numerous delicate ducts opening on the surface of the ejaculatory duct and probably constitute a prostate gland. Outside this gland lie heavy longitudinal muscle bundles, a part of the body muscula-

ture. The cells of the gland are embedded in the innermost of these muscle-bundles. The lumen of the ejaculatory duct is lined with a thin cuticula, beneath which are found cuticular muscle fibres and subcuticular cells. Outside this layer is a thick mass of circular muscle fibres, and outside these a heavy longitudinal layer of fibres. To this coat are attached the radially arranged muscle fibres above described, inserting in general at the angle shown in figure 65, plate 43.

Spermatogenesis.—The follicles of the testes are lined by a syncytium in which are embedded rather small rounded nuclei of the spermatogonia. The middle of the follicle is filled with dividing cells and developing spermatozoa. No attempt has been made to work out the details of the process of spermatogenesis. It may be mentioned that in none of the preparations observed by the writer were there any indications of amitosis, but several mitotic figures were observed. The mature spermatozoon is a slender thread tapering at the posterior end, with a well-marked head, several times the diameter of the body and staining intensely (pl. 41, fig. 50).

The Ovum and Oögenesis.—Unfortunately the writer has seen no young specimens of *Gyrocotyle*. While there has been great variation in size, in all individuals the uterus has been full of developing embryos which mark the specimens as sexually mature. Lönnberg, the only investigator who has had the good fortune to work with the immature form, described the ovaries in the young individuals as follows:

“Das Ovarium hat bei jüngeren Individuen eine nicht gewöhnliche Gestalt, indem es viel mehr traubig gelappt als bei anderen Cestoden ist. Es besteht also in diesem Stadien aus kleinen rundlichen Follikeln, die durch weite Ausführungsgänge zu Trauben vereinigt werden, und diese Trauben erster Ordnung werden durch ihre Ausführungsgänge zu Trauben zweiter Ordnung verbunden. Alle Trauben vereinigen sich zu je einer Sammlung aufschmelzen aber allmälig die Trauben zu unregelmässigen Lappen zusammen und es scheint daher nicht treffend, wenn Spence auf seiner schematischen Figur ein so distinkt traubenförmiges Ovarium bei einem Tiere mit von Eiern prall gefüllten Uterus zeichnet.”

Spencer (1889, p. 144) dealt with sexually mature forms, but found two stages of reproductive activity:

“In the first-mentioned the ova were evidently passing down into the uterus, in which they were but very slightly developed. The ovaries

consequently were full of fully formed ova, having the nature of distinct cells with clearly defined nuclei. In the second the uterus was full of much more highly developed embryos, and no ova, apparently, were passing into it. In this case the ovaries were evidently in the act of developing a fresh supply of ova. Each consisted of a mass of protoplasm containing nuclei, evidently dividing rapidly, whilst the outlines of the cells could only here and there be seen with anything approaching to clearness. Each little ovary has thus, when the ova are not fully formed, the structure of a polynuclear mass of protoplasm, which only subsequently becomes divided up into a number of distinct cells.¹

In all the preparations studied by the writer, the ovaries contained at the same time both fully formed and developing ova; the uterus contained young embryos in its most posterior coils, and older ones towards its anterior opening. It seems that in *G. fimbriata* the process of egg formation goes on uninterruptedly the year round, rather than in a rhythmical fashion, as indicated for *G. rugosa* by Spencer's observations. This may be correlated with the fact that apparently the period of intra-uterine life is longer in *G. rugosa* than in any other species, this being the only form in which the uterus contains hooked embryos.

Each follicle of the ovary is surrounded by a fibrous layer, called by Lönnberg the "tunica propria," continuous with the walls of the oviducts into which the ova are discharged. Plate 41, figure 52 represents a typical follicle with ova in early stages of development. There is a syncytium containing small, round nuclei with reticular chromatin and either a very small nucleolus or none whatever. The other half of the same follicle is cut up into cells with definite walls, denser cytoplasm, clear nuclei nearly double the size of those in the syncytium, with dense marginal chromatin reticulum and very large excentric nucleolus. Plate 41, figure 53 represents stages intermediate between these two, showing the growth of the nuclei and particularly the appearance of a large extra-nuclear body, staining

¹ Dr. M. Hungerbühler's "Studien an *Gyrocoyle* und Cestoden" (1910) was received too late for its results to be incorporated in the body of this paper. He makes the suggestion, based on the facts above quoted mentioned, that Spencer was dealing with two different species of *Gyrocoyle*, that is, with *G. urna* and *G. rugosa*. While this explains numerous discrepancies in Spencer's account, and while my own results show the presence of two species of *Gyrocoyle* in one species of *Chimaera*, yet the forms described by Spencer differ widely in several essentials from *G. urna*, and Hungerbühler's grounds for concluding that one of Spencer's forms was *G. urna* do not seem adequately to account for these differences.



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Watson: *The Genus Gyrocotyle*.

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by most methods as deeply as does the nucleus but easily distinguishable from it in strongly decolorized haematoxylin preparations, and also in borax carmine-Lyon's blue preparations. Plate 41, figure 54 shows the origin of this body as an extruded nucleolus, distinguishable even when within the nuclear membrane from the chromatin nucleolus proper. Probably only one such body, or "yolk-nucleolus," is formed during the development of the ovum. In fully formed ova this yolk-nucleolus has greatly decreased in staining intensity, appearing as a mere shadowy ring with a dark center (pl. 41, fig. 51).

The ripe ovum passes from the follicle into the oviduct where it takes on an irregular elongated form, strongly suggesting amoeboid movements. This form has also been noted by Lönnberg (1891, p. 40). These ova are the largest cells in the body, measuring about 26μ by 15μ . Their cytoplasm is very dense, full of shapeless masses of material. The nuclei are about 12μ in diameter, clear, with heavy deeply staining chromatin reticulum and large round nucleus, from 5μ to 6μ in diameter. The nucleolus is larger than any other nucleus in the body, except those of the ganglion cells of the first order and possibly the nuclei of yolk cells. The large, clear bright nucleus with its dense deep-staining nucleolus makes the ovum easily recognizable even under low magnification.

The processes of maturation, which have not been observed, probably occur after the ova reach the receptaculum ovarium. Division of oögonia in the follicles of the ovary appears to take place by true mitotic division. Equatorial plates and anaphases have been observed, but no attempt has been made to work out the phases of mitosis. There are no indications of amitosis, either here or in the follicles of the testes. It seems probable from the evidence in *Gyrocotyle*, that Child's (1907) amitotic figures are the result of confusing the "yolk-nucleolus" with the nucleus proper. Such figures as are shown in plate 41, figures 52, 53, 54, could easily be taken for unequal mitotic divisions of the nucleus, were it not for the differential staining.

The vitellaria are follicular, each follicle being surrounded by a fibrous tunica propria as in ovary and testes. The early stages of yolk-cells resemble those of the young ova. A single

follicle frequently contains a great variety of stages. Near one margin are found scattered nuclei in a syncytium; the rest of the follicle is filled with cells with well-defined walls and full of yolk-spheres (pl. 41, fig. 49). The cells are large, about 20μ , with round clear nuclei, dense marginal chromatin and a round central nucleolus. The cytoplasm is reduced to a thin marginal layer in which the nucleus is embedded. The body of the cell is packed with yolk-platelets, from $\frac{1}{2}\mu$ to 2μ in diameter, granular in composition, and staining rather faintly except with Lyon's blue and toluidin blue, with both of which the platelets stain very intensely. The whole cell breaks out of the follicle and enters the system of yolk-ducts, through which it makes its way to the yolk-reservoir and thence to the uterus. The yolk-plates have been observed by me only within a nucleated cell. The cell as a unit becomes one of the components of the compound egg formed in the uterus.

This statement is not in agreement with Lönnberg's description of conditions in *G. urna*. He says: "Die Dotterzellen zerfallen schliesslich, so dass nur die Körnchen durch die Gänge zu den Eizellen gelangen." That is, only the yolk-platelets, not the yolk-cells themselves, enter into the composition of the uterine egg. Aside from the fact that yolk-ducts, reservoir, and the beginning of the uterus are all full of typical nucleated yolk-cells, the most cursory examination of the early coils of the uterus shows that the eggs, even before the shell is completely formed, are multicellular. Lönnberg saw this, but interpreted it as evidence of a very early cleavage of the ovum. "Die Eifurchung tritt sehr frühzeitig ein, so dass man Eier findet, deren Schalen noch nicht fertig gebildet sind, aber wo das Embryo schon gebildet ist." But a careful examination of such an early uterine egg shows that it contains cells of two kinds, one having the characteristic size, staining reactions and nuclear structure of the ovarian ovum (*ov.*), and the others typical vitellarian cells (*yk. c.*, pl. 9, fig. 47). Cleavage of the ovum does not begin for some time after the shell is completely formed. Spencer's (1889, p. 145) observations concerning the yolk-gland and his figures of yolk-follicles are very puzzling. His statements are as follows:

"A difference of structure has been noted above in the case of the

ovaries of the two examples examined, containing embryos at different stages of development in the uterus, and a curious difference obtains also in the yolk-glands of the two forms. In the one containing highly developed embryos the yolk-glands, like the ovaries, are evidently providing a fresh supply of material in prospect of the next period of reproductive activity. Each consists of a mass of cells, the outlines of which are somewhat more clearly marked than in the case of ovaries, with large nuclei evidently undergoing division. The cells are remarkably similar to ova, but the relative size of the yolk masses and their definite superficial position renders them distinct from the ovaries. In the case of the form containing the ova passing down into the uterus, the yolk-glands are in a much more advanced stage. Each is filled with a mass composed partly of distinct yellow globular bodies, and partly of nucleated cells. So far as can be seen there are no definite "shell-glands" present; all the other structures connected with the reproductive organs could be distinctly made out by means of sections, and presumably shell-glands would have been able to be recognized if they were present as distinct and separate structures. In plate 13, figure 2, is represented a portion of the first part of the uterus, in which evidently the shells are being formed around the ova. In addition to nucleated cells, the uterus contains very numerous little drop-like yellow structures, which resemble exactly those which have been previously described as present in the yolk-glands. It appears as if these, as it were, "ran together," and formed a case enclosing certain of the nucleated cells, some of which are ova, and some probably cells from the yolk-glands which will serve as food for the developing ova. This appears to be the only construction which can be placed upon the appearances."

Failing to find any shell-glands in *G. rugosa*, Spencer's hypothesis (though not definitely stated to be such) seems to be that both shell-material and yolk-platelets are formed in the yolk-glands, as indicated in his plate 13. Nothing resembling this type of follicle, or indicating such a function of the vitellaria, has been seen in *G. fimbriata*. It is hard to believe that Spencer could have observed so delicate and obscure a structure as the network of yolk-duets in the region of the receptaculum seminis, and overlooked the large and unmistakable masses of the shell-glands, had they been present in *G. rugosa*. Lönnberg (1891), who observed the shell-glands in *G. urna*, suggests that Spencer mistook the central mass of the shell-glands for the central part of the ovary. This suggestion is rendered less plausible by the fact that the main mass of the shell-glands lies, not in the median line, but laterad of the receptaculum seminis, and is simply marked off from the mass of the ovaries. A revision of Spencer's material seems to be the only way in which the discrepancy in observations can be explained.

V. FORMATION OF THE COMPOUND EGG AND CLEAVAGE OF THE OVUM.

The formation of the compound egg of *Gyrocotyle* in the first coils of the uterus has been described above. The completed egg presents the appearance shown in plate 41, figure 47, taken from the fifth coil of the uterus. Cleavage begins very shortly; at the same time the walls of the yolk cells become less definite and their nuclei fainter. There is no indication of cleavage of the yolk-cells. The mass of cells resulting from cleavage of the ovum appears to be a syncytium (pl. 41, fig. 48); this mass increases in size with the diminution of the yolk cells. It is impossible to make out cell walls or to discover any orderly arrangement of the nuclei, in the preparations available. The eggs cannot be made sufficiently transparent for study *in toto*; and the shells are so resistant that no successful infiltration with paraffine was obtained. The best preparations, and the ones on which these statements and figures are based, were celloidin sections stained with Delafield's hematoxylin. The egg-shells show no opercula, and no trace of hooks on the embryo could be discerned. *G. rugosa* seems to be the only member of the genus which possesses hooked embryos in uterine eggs.

The eggs when extruded are surrounded by a gelatinous substance which forms a jelly on contact with sea-water. They are discharged with considerable force. The discharge has been observed repeatedly when the intestine of the host was first slit open, and also when the animal was changed from one solution to another. Eggs are always found in the intestinal contents of *Chimaera* infected with *Gyrocotyle*. The eggs when first discharged are white and glistening, resembling finely cut sand-grains. They are about .095 mm. by .065 mm. and ellipsoidal in shape. The size varies widely in eggs from the same individual, discharged at the same time, ranging from .075 mm. to .112 mm., in longest dimension.

The newly discharged eggs do not possess opercula (pl. 38, fig. 41). There is a faint differentiation occasionally seen at one pole of the egg, but nothing which could be definitely identified as an operculum has ever been found in fresh eggs. In speci-

mens which had begun to decay in the intestines, and in preparations made by Von Rath's method, a perfectly definite and clearly marked operculum was found (*operc.*, pl. 38, figs. 38, 39, 40). This does not appear to be comparable to the operculum figured by Haswell (see my plate 47, figure 81). Its margins are finely toothed, and the shell is somewhat thinner in the opercular cap than elsewhere.

VI. EXCRETORY SYSTEM.

The network of excretory canals, so richly developed in *Gyrocotyle*, is one of the first features to strike the eye in observation of the living animal. Wagener (1851) saw and described it, and noted particularly its wonderfully elaborate development. The excretory system consists of the following parts: (1) "flame-cells," (2) capillaries, (3) excretory canals distributed outside the inner longitudinal muscle layer, (4) excretory canals lying within and among the fibres of the inner longitudinal muscles.

The "flame-cells" (pl. 43, figs. 62, 63) are large, with swollen base in which lies an oval nucleus with rich, deeply-staining chromatin reticulum. The surrounding cytoplasm is granular, occasionally vacuolated, and stains as heavily as does that of the gland-cells. Running apparently from the apex of the nucleus is a fine thread, extending for some distance through the hollowed-out body of the cell. Each flame-cell thus forms an intracellular canal, which leads into a capillary. These flame-cells are found only in the outer layers of the body in what has been described as the "intermediate" region, within the subcuticular layers and outside the inner longitudinal muscle mass. Neither Spencer (1889) nor Wagener (1852) found any such structures; Lönnberg (1891) found them, but tells us nothing about them, except that they lie in the "Rinden-schicht."

The capillaries are the fine tubules into which the intracellular ducts of the flame-cells lead. They have very thin walls, and differ from the excretory canals in not having a cuticular lining or a muscle layer. They are found throughout the body wherever flame-cells appear.

The excretory canals lying outside the inner longitudinal muscle mass differ from those lying within this layer chiefly in

size. They are lined with a cuticula resembling that covering the body, and are surrounded by a well-developed band of circular muscle fibres (*circ. musc. l.*, pl. 11, fig. 60) resembling in size and shape the cuticular longitudinal fibres of the body. Outside of this circular muscle layer is a mass of parenchyma fibres passing in the same direction. Nuclei are scattered about irregularly in the neighborhood of this layer, but often at some little distance from it.

In the larger of these canals, a large tuft of cilia projects into the lumen, through a break in the cuticular lining, running the whole length of the canal. These ciliated canals receive the smaller non-ciliated ones. The non-ciliated canals are plainly to be seen in the living animal in the lateral frills, in close relation to the follicles of the vitellaria, emptying on the one side (lateral) into a small non-ciliated "sinus terminalis" (Wagner) and on the other side (medial) into a ciliated canal of about twice their own diameter (pl. 35, fig. 20). Still further mediad, near the base of the lateral folds, is a second ciliated canal, of the same size and appearance as the first. In it, however, the waves of motion traverse the cilia in the opposite direction from that taken in the more lateral canal. Thus, if in the outer one waves pass from anterior to posterior, in the inner one they run from posterior to anterior. The motion is almost incredibly swift and very regular.

The largest excretory canals lie within the central core of the body, among the inner longitudinal muscles, the ovaries and testes. Running the length of the body, on either side of the uterus, is a very large ciliated canal, the largest in the body. The structure of these canals is like that of the smaller peripheral canal described above, except that the lining is thicker, the muscular layer better developed and nuclei more numerous in the neighborhood of the wall of the canal. In no case has it been possible to recognize any connection between the cilia of the canals and the neighboring nuclei, such as was figured by Lönnberg (1891, Taf. 3, figs. 39, 40).

Around the anterior margin of the acetabulum there is a fairly well-defined ring-canal, receiving many small anastomosing longitudinal branches. Its diameter and relations shown

by sections do not indicate that it is connected with the central canal-system, but rather with the peripheral non-ciliated system of the lateral folds. The same is true for the dense network of non-ciliated canals found in the posterior rosette. This rosette region is riddled through and through with small canals, much like capillaries in size and structure of wall. No flame-cells appear in this region. A ring-canal appears in the "neck," at the level of the canal opening. Like the acetabular ring, this appears to be immediately connected with the peripherally situated canals, and through them with the deeper-lying larger vessels (*ant. ex. r.*, pl. 36, fig. 26.)

In several specimens a dilation of one of the large longitudinal canals has been found in the region of the vaginal opening, usually posterior to it. These dilations take the form of a thin-walled sphere, into which the large canal empties, containing droplets of a structureless yellow material. It is certain that this "bladder" is not a constantly occurring structure. No external openings have ever been found, except by Spencer (1889) on *G. rugosa*: "Wagener was unable to find any external opening of the excretory system, but, after long searching, I have been able to find two unmistakable openings on the ventral surface, one on either side of the body, slightly in front of the opening of the uterus to the external surface." Lönnberg (1891) was unable to find these openings; the writer has never seen them. But it seems highly probable that these temporary "bladders" may burst through the wall of the body to form a temporary external opening, closing up after the collapse of the "bladder," due to the discharge of its contents.

VII. NERVOUS SYSTEM.

The nervous system of *Gyrocotyle* is of great interest with reference to the problem of orientation, both in the genus itself and in merozoic cestodes. It may be divided into central and peripheral parts, according to the muscle layers with which the nerve stems are related. The sense in which the phrase "central nervous system" is used is of course quite distinct from the meaning usually attached to it when applied elsewhere, as for example to vertebrates. Neither should this use of the term be

confused with that advocated by Cohn (1898) for merozoic cestodes. He believes that all of the longitudinal nerves, together with their transverse connections in scolex and proglottides, constitute the central nervous system. The branches from these to the various organs and to the surface of the animal he regards as the peripheral system. While all the evidence indicates that such a division would be justifiable in *Gyrocotyle*, it is not in this sense that the terms are here used, but purely with reference to position, not at all with reference to structure or function.

The *peripheral nervous system* consists of eight longitudinal stems, lying in the intermediate muscle layers, just outside the outer longitudinal set of fibres, and communicating with the central system by means of the anterior nerve ring around the margin of the acetabulum. There are no ganglion cells in these strands; they are very small and exceedingly difficult to trace. With borax carmin and Lyon's blue they stain a very clear light blue, and can be recognized with some ease in the neighborhood of the acetabulum, especially near their junction with the anterior ring. These strands have not been previously described. They innervate the intermediate muscle layers (outer transverse and outer longitudinal), wherever these occur in the body proper, in the inner layers of the acetabulum, and in the inner layers of the funnel.

In dealing with the central system it is important to remember and recognize the existence of these extra-central nerves, for it is only when the central system is clearly distinguished from the others that the relations of its parts become intelligible. It is perhaps because of their failure to take account of this division that the results of investigators of the nervous system of *Gyrocotyle* have shown so little agreement in details.

It is hardly necessary to say that the study of the nervous system by means of serial sections, already made difficult by the great contractility of the body, is rendered a much more serious problem by the necessity of dealing not with two stems, their branches and connectives, but with six or perhaps ten such stems. To determine whether a complete ring is present in any part of the body becomes a task of serious difficulty, and indeed one impossible without the assistance of the relations of the different

sets of nerves to the muscle layers, which can always be distinguished from one another.

The *central nervous system* lies within (mediad to) and among the inner longitudinal muscle-fibres, and within (mediad to) the large longitudinal excretory canals. It consists of the following parts:

1. Two lateral longitudinal stems.
2. An anterior bridge commissure and an anterior ring commissure, in the acetabular region.
3. A posterior bridge and two ring commissures, joined by eight longitudinal connectives.

The nervous system was first recognized by Wagener (1852), who saw only the anterior commissure. Monticelli (1889a) and Spencer (1889) recognized the posterior commissure. According to Spencer, this commissure is continuous around the canal, forming a complete ring surrounding the canal; the dorsal half of the commissure extending farther posterior than the ventral half. According to Monticelli this is not the case. He found that on the ventral surface the two parts did not unite, but merely ran alongside each other, then separating passed posteriorly, each ending independently in the margin of the "Trichter." Both these investigators agree in placing the anterior, heavy and indubitable part of the commissure on the same surface as the canal opening, *i.e.*, the ventral face (dorsal of Spencer and Monticelli). This puts the anterior (acetabular) commissure on the opposite surface from the posterior (scolex) commissure.

Lönnberg (1891) described both commissures as lying on the ventral surface. He found the posterior commissure to be a bridge, not a complete ring, posterior to which the longitudinal stems are continuous to the margin of the funnel, where each breaks up into many branches, which probably form by their anastomoses a ring about the margin of the funnel opening. Thus his account differs from Monticelli's in (1) the presence of a marginal ring at the posterior extremity, and (2) the absence of any statement of the near approximation of the posterior nerve stems to each other posterior to the commissure. It differs from Spencer in the first point, and also in the absence of any indication of the completion of the posterior commissure to form

a ring surrounding the canal. Lönnberg also differs from Spencer and Monticelli in placing the posterior commissure "ventrally." The apparent contradiction in these results is due to incomplete rather than erroneous observation.

The longitudinal nerve stems or lateral connectives (*long. n. st.*, pl. 39, fig. 42) lying in the dorsal half of the central region of the body, run from the anterior to the posterior commissure. They are separated from each other by one-third of the width of the body in the anterior quarter of the body, but spread further apart at the level of the birth pore, lying near the lateral margins of the uterus. In the region of the ovaries they approach the median line again. Each stem gives off two sets of branches, one in the sagittal and the other in the horizontal plane. These branches are heaviest and most profuse in the regions of the ovaries and the testes.

The *acetabular nervous system* consists, as elsewhere in the body, of a central and peripheral portion. The peripheral system comprises eight longitudinal strands with many anastomosing branches. These strands innervate the peripheral muscle layers of the body, and the homologous muscle layers of the acetabulum. They come into relation with the central nervous system by means of the anterior ring in the margin of the acetabular opening (*acet.*, pl. 39, fig. 42.)

The *central system* includes an anterior bridge commissure, lying just in front of the posterior margin of the acetabulum on its dorsal surface; a pair of anterior lateral stems with branches; and an anterior nerve ring (pl. 39, fig. 42). The commissure forms a bridge between the two longitudinal nerve stems. There is a ganglionic enlargement of the lateral stem at a point where it is joined by the bridge commissure. The commissure is in the shape of an arch, enlarged at the ends and smaller in the middle of its course. Its mass with respect to the rest of the body varies widely, perhaps with the state of contraction of the animal; it is fairly constant with respect to the nervous system as a whole. No branches are given off from the commissure itself. The marginal ganglionic knots are about double the diameter of the lateral stem (*ant. br. comm.*, pl. 39, fig. 42). They are enlargements of the lateral stems, beginning at the point where the

anterior bridge commissure is given off and reaching their greatest size in that region. Anteriorly they pass into the anterior longitudinal stems, extending fully a third of the total distance from the commissure to the anterior ring. From each ganglion the following branches are given off (pl. 36, fig. 27).

1. An anterior lateral nerve stem, a prolongation of the anterior nerve stem in front of the anterior bridge commissure, runs forward along the dorso-lateral margins of the acetabulum. From these stems there are given off dorsal, ventral and lateral branches to the body musculature, and median branches to the outer coat of the acetabular muscles. Certain branches from the dorsal surface run forward, to the dorsal sensory ridges later described, and from the ventral surface of each stem near its anterior extremity a large nerve runs forward ventro-laterally to the sensory pits on the ventral surface. At the anterior extremity of the worm near the acetabular opening, each lateral nerve stem divides into two branches which pass, one ventrad, the other dorsad, at right angles to the longitudinal stem. These nerves break up in the median line to form the anterior nerve ring.

2. Four nerves are given off from the ventral surface of the knot, two of which are directed posteriorly and two anteriorly. The posteriorly directed pair of branches are distributed to the follicles of the testes (*test. n.*, pl. 36, fig. 27). The anteriorly directed pair pass around the posterior margin of the acetabulum on its ventral surface and send out branches on this surface.

3. Four nerves arise from the dorsal surface, running forward and laterally into the inner longitudinal muscles.

4. Two nerves arise from the lateral surface of the ganglion, one running forward and ventrally, the other towards the dorsal surface, into the central musculature of the body and the vitellaria.

5. Several nerves are given off from the anterior face of the ganglion and run forward along the surface of the acetabulum to innervate the outer meridional acetabular muscle coat (the homologue of the inner longitudinal coat of the body musculature).

The Anterior Ring Commissure.—The anterior end of the worm is pierced by a round opening into the cavity of the

acetabulum. The circular margin of this opening is rounded and thick, due to the presence of a heavy sphincter. Surrounding this opening, within the sphincter of the margin, is the anterior excretory ring and the anterior nerve ring. This is formed as described by dorsal and ventral terminal branches of the anterior lateral stems, united in the median line by a dorsal and ventral anastomosis. This ring is thus composed laterally of a single large nerve, but in the median line of many small anastomosing threads (pl. 39, fig. 42). In its lateral portions at the points of junction with the lateral nerve stem, there is a slight enlargement in which typical ganglion cells are present. From the ring are given off nerves ramifying in the margin of the acetabular opening, and in the outer layer of the acetabular muscle coat. The ring also receives the peripheral stems mentioned above.

The Central Nervous System of the Rosette and Canal.—The posterior rosette may be considered as composed of two parts,—a funnel and a canal. The wide-mouthed funnel with glandular, much folded walls is circular in cross-section, and roughly V-shaped in sagittal section, the point of the V being directed anteriorly. That is to say, the course of the funnel tube is almost straight forward through the center of the body (pl. 46, fig. 76). Its posterior margin is bordered by the frills which make up the posterior rosette. At the base of these frills there is a thickening of the walls of the funnel commonly referred to as the neck of the rosette, due to the formation of a sphincter by the inner transverse muscle. This funnel leads into the canal, a narrow, non-glandular region, passing a little anteriorly and almost directly ventrad to open on the ventral surface of the valve-like canal opening. The region where the canal joins the funnel, the apex of the V, will be called the tope, from the corresponding region of an ordinary funnel. The walls of the canal itself show no central innervation. There are apparent fine fibres of the intermediate and cuticular nerves but no branches of the central system. From the tope of the funnel posteriorly the walls of the passage are weakly innervated by a complicated set of commissures, stems, and branches, all belonging to the central system, consisting of the following parts:

1. A posterior bridge commissure connecting laterally situated ganglionic knots.

2. A proximal ring commissure directly connected with the posterior margin of the ganglionic knots.
3. A distal ring commissure, connected with the proximal ring by eight connectives.
4. Anastomoses between these connectives in the lateral walls of the funnel.
5. Eight branches running posteriorly from the distal ring commissure into the folds of the terminal rosette.

The main longitudinal stems lie as above noted in the dorsal half of the central region. At a point just posterior to the tope, close to the wall of the funnel, each stem enlarges to form a ganglionic knot (pl. 35, fig. 17). These knots are connected dorsally by a transverse bridge which is fairly large laterally, but narrows to the merest thread in the median region, not distinguishable with a magnification of less than 300 diameters. The ganglionic knots at the ends of this bridge commissure pass diagonally across the lateral walls of the cavity. This forms the "bow-commissure" of Spencer. Each ganglionic knot divides into two main branches, a dorsal and a ventral, which pass toward the median line to join similar branches from the opposite side, thus forming the proximal ring commissure, lying about half-way between the neck or sphincter region and the tope of the funnel. It was probably the ventral half of this ring which Spencer regarded as forming the "dorsal" region of his bow-commissure, embracing the funnel. Lönnberg's "ventral" commissure was probably the dorsal half of this same ring, plus the lateral ganglionic knots of the posterior commissure, the half-ring and knots being connected by one of the primary lateral connectives to be described later. The middle third of the dorsal posterior bridge commissure is so delicate that it is easily overlooked. However, the continuity and independence of both the dorsal commissure and the dorsal half of the ring can be easily demonstrated in serial sections with a magnification of about 300 diameters.

In the neck or sphincter region there is formed a second ring which completely encircles the posterior margin of the funnel at the base of the frills. This posterior ring is connected with the proximal ring by eight connectives (*lat. long. conn.*, pl. 35, fig.

17). Of these, the two lateral pairs are derived from the primary longitudinal stems, each divided into two and continued posteriorly from the ganglionic knots. The two lateral connectives of each side are interconnected by anastomosing branches, lateral and irregular, nearly parallel to the proximal ring, and frequently quite as heavy. The dorsal and ventral median pairs, lying in the median third of the funnel wall, extend only from the proximal ring to the distal ring. From the distal ring branches run out into the frills at the points where the longitudinal connectives enter the ring.

Distribution of Ganglion Cells.—No attempt has been made to deal with the histology of the nervous system, further than is necessary for understanding the significance of the structure of the ganglionic knots at the lateral margins of the anterior and posterior commissures. The nerve stems, both longitudinal and peripheral, are composed of exceedingly delicate fibrils, woven together in a dense meshwork (pl. 34, fig. 16). Around the stem is a covering of nucleated parenchyma fibres, or sheath cells. There are no nuclei within the meshwork. At intervals along the two main lateral stems, where branches are given off, there appear just inside these "sheath cells" a cluster of cells having homogeneous cytoplasm and oval, clear nuclei, with a few chromatin nucleoli (*gang. 1st.*, pl. 44, fig. 67). These correspond to the "first type" of ganglion cells described by Pintner (1880) and by Niemiec (1886). They occur only at the margins of the main lateral nerve stems and in the nerve rings: the anterior ring, the proximal and distal ring commissures. In the ganglion knots there occur very large cells, with coarsely granular, intensely staining cytoplasm, and a large, clear nucleus containing one large and several small chromatin nucleoli (pl. 44, fig. 66). With Lyon's blue these cells stain a dark violet blue quite distinct from the clear "Himmelblau" as Lönnberg calls it, of the the fibrous tissue. These occur only in the ganglion knots of the anterior and posterior bridge commissures, not at all in the median sections of the commissures, in the rings, or lateral stems. They are not numerous, their total number not exceeding seventy or eighty. They correspond to the second type of cells described by Pintner and by Niemiec, commonly referred to as giant cells.

VIII. SENSE ORGANS.

The presence of sensory end-organs in cestodes has been several times suggested, but never established to the satisfaction of investigators in general. Lang (1891) says "The cestodes no longer possess any specific sensory organs." Braun (1894) in Bronn's *Thierreich* (p. 1300) quotes Blumberg (1877) as observing nerve endings in the limiting membrane or cuticle of the *Taenia* of horses. These endings are in the form of delicate threads terminating in a swollen knob. Braun thinks that, considering Zernecke's observations, it seems probable that Blumberg saw actual nervous end-organs. Linton (1891) briefly describes an organ of hearing in *Otobothrium crenacolle*, as a small structure covered with hairs, situated on the bothridia. Beyond these, and Schiefferdecker's (1874) interpretation of flame-cells as nerve endings; there are no references to sense-organs in the literature of cestodes, in so far as that is known to the writer.

In *Gyrocotyle* the whole acetabulum functions much as does the proboscis of the rhabdocoelan *Proboscidea*, as a highly efficient organ of exploration, or one might say of touch. While the whole surface of the acetabulum is richly innervated, there are on the margin of the opening of the acetabulum two ridges with a peculiar and significantly rich nerve supply, and two shallow pits in which lie flat plates of nervous tissue, end-organs of a pair of heavy branches from the anterior lateral stem above referred to.

1. *The Sensory Ridges or Papillae*.—These lie one on each side of the latero-dorsal margin of the acetabular opening. A nerve from the anterior lateral stem spreads out within each "papilla," its branches running to the base of the very thin limiting membrane.

2. *The Sensory Pits (sens. pits, pl. 36, figs. 23, 25)* lie farther laterad than the papillae, and on the opposite or ventral surface of the acetabular margin. They consist of a definite depression, covered with a differentiated membrane, immediately beneath which lies a plate of nervous tissue, formed by a very heavy branch from the anterior longitudinal nerve. This does not break up but ends abruptly as a plate of nervous tissue

immediately beneath the limiting membrane of the pit. These pits stain an intense blue when the living animal is treated with methylen blue. They take up the stain quickly and hold it for several hours after removal from the staining medium. The function of these pits is totally unknown, but the presence of central nervous tissue immediately beneath their surface indicates their possession of some sensory function.

E. GENERAL DISCUSSION.

This investigation was undertaken and carried out in the hope of obtaining evidence which would definitely settle the question of antero-posterior orientation. This evidence was sought along three lines: (1) morphological relationships of organs, in themselves and compared with other platyhelminths; (2) behavior of the living animal; (3) embryological history. The writer has unfortunately failed to find any extra-uterine embryological material, and has no evidence from this source to offer. The fact that *Chimaera colliei* can not be kept in aquaria, even large ones, with any measure of success (Dean, 1906, p. 16) makes the life-history a hard problem to attack. I am convinced that we have thus far no hint whatever as to the intermediate host of *Gyrocotyle*. The occurrence of decaying, sexually mature forms in *Mactra edulis* has, it seems, no bearing on this question. The youngest forms reported, the only immature ones in fact, are the young individuals found by Lönnberg in the spiral valve of *C. monstrosa*. This fact indicates that the worm enters the host in a sexually immature condition. The fact that no hatched embryos have been found in the intestinal contents of *Chimaera* indicates that *Gyrocotyle*, like other cestodes, has at least two hosts. Further than this we know nothing of its life-history.²

Conclusive morphological and functional evidence bearing on the question of orientation has been found in abundance. In the course of this work, evidence bearing on certain other questions

² The discovery by Hungerbühler (1910) of cysticercoids in the parenchyma of *Gyrocotyle rugosa* is a recent addition to our knowledge of the embryology of the genus. The embryo resembles the ten-hooked embryo already figured by Spencer as an extra-uterine embryo. Its position (near the uterine pore) suggests that the wall of the uterus may have given way in that region in the preparation of the specimen.

of interest to students of the phylum has been found; this will be briefly discussed before proceeding to consider the main problems of orientation.

I. CUTICULA.

The question of ectodermal origin of the "cuticula" or limiting membrane of the body, and the significance of the "subcuticular cells" in the trematodes and cestodes has been recently reviewed by Professor Pratt (1909). Blochmann's theory, regarding the subcuticular cells as a sunken epithelial layer, and the limiting membrane as a true cuticula, such as is found in arthropods and annelids, Pratt considers completely discredited by various pieces of embryological and morphological evidence. He considers the "cuticula" to be nothing but a closely matted layer of parenchyma fibres, from which the nuclei have disappeared. The observations made on *Gyrocotyle* seem to bear out this view of the limiting membrane. Of particular interest are the conditions of the vagina, receptaculum seminis and uterus. Here the lining of these ducts is in direct continuity with the cuticula at their openings; there is a gradual transition from this cuticular lining to one of comparatively loose-matted fibres and indefinite boundaries, containing unmistakable parenchyma nuclei and passing on its inner surface indistinguishably into a typical parenchymatous net in which lie muscle fibres. This same transition can be seen on the inner surface of the folds of the posterior rosette. Furthermore, nowhere in *Gyrocotyle* have I found a definite layer of epithelial cells. Such tissue, described by Lönnberg for the ducts of the reproductive system, resolves itself in favorable preparations and under high magnification into the dense parenchymatous layer, fibrillated and without cell-walls, above described.

One statement made by Pratt in support of this view of the cuticula as not associated with the subcuticular cells is not borne out by conditions in *Gyrocotyle*. He says: "If now the cuticula is the product of the underlying subcuticular cells, we should expect to find some special development of them beneath the hooks and spines, especially where these are very large, just as in the integument of insects a cuticular hair or scale is invariably

situated over the enlarged hypodermal cell which produces it. Nothing of the sort exists in trematodes and cestodes. The subcuticular cells beneath the hooks and spines do not differ in size, number or arrangement, from the adjacent cells and in the monogenetic trematodes, which are often provided with gigantic hooks, no subcuticular cells at all are present."

In *Gyrocotyle* the subcuticular layer of cells is much increased in thickness in the neighborhood of a spine and is closely related to it.

A question of far greater difficulty is that of the function of the subcuticular cells. If not related to the formation of the cuticula, what is their function? Pratt makes two suggestions; first that they are secretory in function, forming an antibody for the protection of the worm from the chemical action of the medium in which it lives. This is supported by the fact that these cells are altogether lacking in monogenetic trematodes. A second suggestion (see Looss, 1894), is that these cells constitute an undifferentiated embryonic layer, from which new cells of various tissues are formed during the lifetime of the animal. The only evidence in support of this theory is the statement that in certain individuals known to be of advanced age, the subcuticular layer was greatly reduced.

The glandular theory finds no definite support in the conditions in *Gyrocotyle*. The unmistakable gland cells here present are found as above noted in the central core of the body, not in relation to the peripheral layer. The statement made by previous investigators that the subcuticular layer gives rise on the inner surface of the rosette folds to gland cells has not been verified in the writer's preparations. However, this does not militate against the possible glandular nature of these cells. The intense staining reaction of the cytoplasm of at least some of these cells recalls the appearance presented elsewhere by unmistakable gland cells.

Looss's suggestion seems hardly susceptible of proof or disproof. It is difficult to believe that the layer of cells so closely related in position to the cuticula, varying in thickness with its thickness and increasing in the region of special cuticular structures such as spines, should be totally unrelated to the body-

covering. The conditions of *Gyrocotyle* indicate very clearly that the subcuticular layer is related to the cuticular musculature, and that some at least of its cells are to be considered the myoblasts of the cuticular muscles. There is much in the literature of the subject in harmony with this suggestion; Blochmann (1896) shows in his diagrammatic cross-section of *Ligula* myoblasts lying near the subcuticular layer. He was able to distinguish these cells from the rest of the subcuticular layer. This the writer is unable to do in *Gyrocotyle*. The fact that the cuticular musculature always increases with the thickness of the cuticula, disappearing as the cuticula thins out and passing into the fibrous nucleated layer above described, lends support to the suggestion. In the lining of the receptaculum seminis and the posterior end of the vagina, no subcuticular cells can be seen. These ducts are surrounded by simple nucleated muscle fibres. In the early coils of the uterus, where this same nucleated fibrous lining is found but where cilia are also present, the cilia pass through the fibrous layer and are in connection with scattered nuclei lying just beneath the fibrous lining. Further along the course of the uterus, where a definite non-nucleated fibrous lining has appeared, beneath which lies a cuticular musculature, the subcuticular layer appears, just as it does beneath the cuticular musculature of the body-covering. All the facts available indicate that at least a large part of the subcuticular cells are related, not to the cuticula, but to the cuticular musculature as myoblasts. The subcuticular cells in the neighborhood of the spines are probably related to the protractor musculature of these structures.

II. ORIENTATION.

The question of antero-posterior orientation of cestodes is one of peculiar difficulty. Their endoparasitic and attached mode of life makes it impossible, in general, to settle the matter by the test ordinarily applied, that of the direction of locomotion. The usual custom, reflecting the influence of Leuckart, has been to regard the scolex end as anterior, the free end as posterior. Many early workers, among them Perrier, Grassi, and Blanchard, reversed this orientation, looking on the scolex as

the posterior end. In the Cestodaria, conflicting views as to the orientation of the various genera have long existed, and in the genus *Gyrocotyle* the question never has been conclusively settled. It is of peculiar importance for the problem of cestode orientation in general that these relations should be well established in *Gyrocotyle*, for there is no functional antero-posterior orientation in the adult merozoic cestode and the problem there is one of comparative morphology and phylogenetic development. Since *Gyrocotyle* is in every respect a primitive, relatively simple form, parasitic in one of the most ancient of vertebrates, it seems reasonable to assume that this cestode may give some hint as to the extremity at which the ancestral cestode most probably developed its organ of firm attachment. Observations of the living animal have shown that in *Gyrocotyle* there is still a definite functional antero-posterior orientation, due to the fact that it is not a permanently attached form but is still capable of locomotion.

Diesing (1855) regarded the acetabular end of *Gyrocotyle* as anterior, but his grounds for this decision are not clear. Working with a few poorly preserved specimens, he had little on which to base his conclusions. Wagener (1852), who did careful work on the living animal and on sections, had proposed the same orientation on the basis of the active exploring movements of the acetabulum in the living animal, and of the location of a bridge commissure of the central nervous system at the base of the acetabulum. This orientation was followed by succeeding investigators up to Spencer (1889), who reversed it on the strength of the discovery of a similar and much heavier bow-commisssure at the rosette extremity. He did not observe living material. Lönnberg, working on a large quantity of living and preserved material, followed Spencer in regarding the rosette as anterior, basing this decision on the behavior of the living animal (the stretching out of the rosette and funnel into a long canal which performed exploring movements and is directed forward in locomotion, according to his observation), on the great development of its nervous system in the funnel region, and the greater abundance of ganglionic cells in that as compared with the acetabular commissure, on the direction of the spinules,

which point toward the acetabulum; and also on the fact that the worm is always attached to the rosette extremity, since "cestodes always attach by the head end." Haswell (1902) rejects Lönnberg's and Spencer's view on orientation on the basis of homologies in position between the reproductive organs of *Gyrocotyle* and of merozoic cestodes, to which in his opinion it is very closely related. "The end which bears the sucker is seen as the result of such a comparison, to correspond to the scolex end in the segmented cestode." This homology I regard as unjustifiable, as will be pointed out later. Benham (1891), comparing the reproductive organs of *Gyrocotyle* with those of *Amphilina* and the heterocotylean trematodes, concludes that the acetabulum of *Gyrocotyle* corresponds to the anterior sucker of the trematodes, while the rosette organ and its peculiar proboscis possibly represents the posterior caudal disc of the latter class.

An examination of the literature of the genus thus shows that the orientation of *Gyrocotyle* has been made on the following grounds:

1. Behavior of living animal.
2. Cephalization of the nervous system.
3. Homologies of the reproductive organs with similar structure in the merozoic cestodes and in the trematodes.
4. Direction of spines.

Conclusions based on a consistent and constant functional orientation of the living animal in locomotion and general movements are unquestionably well grounded. Conclusions resting on the cephalization of the nervous system assume that the nervous system will be centralized and most richly developed in the head region. This is true for worms in general and for all platyhelminths which retain in any marked degree the power of moving from place to place. In the trematodes there takes place, however, a remarkable development of ring-commissures in connection with the development of powerful organs of attachment. This is especially noticeable in the large posterior terminal sucker of the heterocotylean trematode (pl. 47, fig. 79). It seems very probable that in a permanently attached form, like the cestode, in which the most powerful and highly specialized musculature of the body is centered in the organ of attachment,

there will be found in that region the greatest and most highly developed mass of the nervous system, quite independent of whether the attached end is the homologue of the ancestral anterior or cephalic extremity or not. Therefore, I am inclined to question conclusions as to orientation based on "cephalization" of the nervous system, unless confirmed by other unquestioned evidence.

The third basis on which the question has been decided, the homologizing of the reproductive organs and openings with those of trematodes or merozoic cestodes, can obviously only be applied in the direction of trematodes as long as the orientation of merozoic cestodes themselves is in question. Furthermore, antero-posterior relations among these structures are fixed and constant for trematodes; while among cestodes the most astonishing variations present themselves.

The direction of the spines is not at all a decisive piece of evidence inasmuch as spines may be quite as useful to the animal if directed anteriorly and serving as a means of attachment, as if directed posteriorly and serving as aids to locomotion.

Wagener's orientation of *Gyrocotyle*, regarding the acetabulum as anterior, the rosette as posterior, is justified in my opinion on the following grounds:

1. This is the functional orientation of the living worm. The rosette end is relatively quiescent while the acetabular end is exceedingly active in exploring movements, is directed anteriorly in well-defined progressive locomotion, and leads in all righting-up movements. The rosette end never leads in locomotion except when shoved backward by the doubling under of the active acetabular end, and performs no movements other than a slight rolling from side to side. This mode of behavior agrees with that described by Wagener (1852) in his original account of *Gyrocotyle urna*; but is totally at variance with Lönnberg's (1891) observations on the same form. This discrepancy is discussed above.

2. The position of the reproductive openings in *Gyrocotyle* as compared with that in the heterocotylean trematodes homologizes the rosette with the posterior sucker. The birth-pore of *Gyrocotyle* is probably, according to Goto's (1891) view of the

uterus in cestodes, the homologue of the female copulatory duct in the Heterocotylea; and the vagina is the homologue of the heterocotylean uterus. This gives exactly similar anterior and posterior relations to the openings of the ducts, the penis-openings being very slightly anterior to the vaginal opening, and the birth-pore lying most posteriorly and some distance to one side of the other two.

3. Further morphological evidence in support of this orientation may be adduced as follows: In the first place there are two pairs of abundantly innervated antero-lateral sensory areas, comparable in structure and location to similar areas in planarians and certain heterocotylean trematodes. In the second place the structure of the central nervous system, when compared with that of the heterocotylean trematodes, affords morphological support to this orientation. The anterior commissure, giving off sensory branches, the main and secondary longitudinal nerve strands, the eight posterior branches and a posterior ring commissure are all common and similarly placed in *Gyrocotyle* and the heterocotylean, as for example in *Tristomum molae*, whose nervous system was described by Lang (1882), (pl. 47, fig. 79). There is added in *Gyrocotyle* the delicate median portion of the bridge commissure and the second ring commissure, which may well have arisen in *Gyrocotyle* in correlation with the increased mass and complexity of the musculature of the posterior organ of attachment, the rosette. Thus a comparison of the nervous system and the position and innervation of the organ of attachment of *Gyrocotyle* with the heterocotylean compels us to homologize the rosette with the posterior sucker of the trematode.

The development of two bridge commissures at the two extremities of the body, approximately equal in abundance of ganglion cells but the anterior supplied with a well-developed median part which is very faint in the posterior one, indicates the manner in which the evolution of the nervous system of the merozoic cestode has taken place. This is, briefly, by the degeneration of the anterior commissure associated with the reduction in the locomotor and sensory functions of the animal, and the great development of the posterior commissure and its

stems and rings, associated with the development of the powerful musculature of the organ of attachment, the scolex.

That this is in harmony with the course of development elsewhere in the phylum is shown by consideration of the probable construction of the nervous system of the primitive turbellarian-like ancestor and the changes it has undergone. Throughout the phylum there is remarkable uniformity in the ground-plan of the nervous system. The primitive structure in the free-living Turbellaria is a sub-dermal plexus of fibres and ganglion cells with a marked concentration of these at the anterior end, and an increase in their number and size on the ventral or creeping surface. This differentiates in two directions; first in the segregation from the plexus of from six to eight longitudinal strands, with irregular transverse connecting fibres; and second, in the increase in size of the main bridge-commissure or brain, and in the development of secondary commissures in the region of the brain and in the neighborhood of specially developed musculature, notably in the pharynx and in organs of attachment. This is to be seen in the remarkable development of the posterior commissure in the heterocotylean in connection with the development of the posterior sucker as the principal organ of attachment. Further, two of the longitudinal nerve-strands, the ventral, become more highly developed than the rest. In the trematodes there are two longitudinal strands, connected near the anterior extremity by a bridge-commissure rich in ganglion cells from the region of which arises a pair of sensory nerves. There are in addition numerous peripheral longitudinal strands and an indefinite number of cross-nerves, anastomosing among themselves to form irregular ring-commissoires about the body. In the posterior region, in close relation to the large sucker, is developed a complicated system of commissures and rings. From this type the nervous system of *Gyrocotyle* has been derived. The longitudinal strands are the same in both; there are however two bridge-commissoires in *Gyrocotyle*. But the sensory function of the acetabulum and the forward direction of that extremity in locomotion, together with the well-developed nature of that commissure throughout as compared

with the delicate median thread of the rosette bridge-commis-
sure, all point to its unmistakable homology with the anterior
commissure of trematodes, and so with the typical "brain" of
the Turbellaria.

The posterior commissure with its accompaniments of com-
plicated rings and connectives has plainly been developed in con-
nection with the musculature of the funnel-shaped rosette-scolex.
This complex development of nervous structure in connection
with a highly developed musculature is strikingly shown
throughout the phylum. The ventral nerve stems, in connection
with the ventral creeping muscles, become heavier, more pro-
fusely branched, than their homologues near the dorsal surface.
The great complexity of the nervous system connected with the
posterior sucker of the heterocotylean has already been referred
to. The development of a posterior commissure, in itself rather
weak, but surrounded by a complex system of rings and connec-
tives such as is found in the rosette of *Gyrocotyle*, is exactly
what would be expected in connection with the development of a
complicated and powerful organ of attachment.

The comparison of the nervous system of *Gyrocotyle* with
that of the merozoic cestodes shows two main longitudinal stems
in both. These are more or less sharply differentiated but always
sufficiently clearly marked to be distinguished from the weaker
longitudinal stems, of which there are four or eight, correspond-
ing to the eight peripheral nerves of *Gyrocotyle*. Near the free
margin of the proglottid, which must be regarded as anterior,
these longitudinal stems are connected by a transverse commis-
sure, in close connection with the transverse canal of the
excretory system. In the scolex there is a heavy ganglionic
bridge-commis-
sure, joining the longitudinal stems, lying midway
between the dorsal and ventral surfaces of the body. Peripheral
to this and in contact with it only at the points where the longi-
tudinal stems enter the commissures, is a more or less complete
ring-commis-
sure. This ring reaches its most perfect develop-
ment in the Taeniidae, but is present in an incomplete form in
Ligula, in the Tetrarhynchidae, and in the Tetraphyllidea.
Distal to this commissure and ring is found a more or less clearly
developed ring joined to the former by numerous connectives,

usually six or eight in number. This ring appears in a rudimentary form in the Tetraphyllidea and in the Tetrarhynchidae; it is well established and clearly marked in the Taeniidae and the Dibothridiata.

It is at once evident that the nervous system of the rosette in *Gyrocotyle* is much more easily homologized with the nervous system of the merozoic cestode scolex than is the nervous system of the acetabular region. There are two serious objections to attempting to derive the nervous system of the cestode scolex from the acetabular bridge-commissoire and its anterior rings. In the first place, the rosette and funnel constitute an efficient organ of attachment, so strikingly like the scolices of many Tetraphyllidea in mode of adhesion and probable developmental history—being formed by partial fusion of the walls of a trough, and later differentiation of the ends of the tube thus formed—that it seems irrational to suppose that two structures of such fundamental similarity could have been developed independently in two groups of organisms as closely allied as are the merozoic and the monozoic cestodes. The acetabulum, on the contrary, never functions as a sucker or organ of attachment; there seems to be no possible relationship between this structure and any of the familiar types of cestode scolex. There is every reason, on the basis of function, derivation and structure for regarding the rosette as a scolex of the phyllidian type. In the second place, there is no “starting-point” for the formation of a ring about the acetabular commissure, no matrix out of which to differentiate the complex rings and connectives of the nervous system of the scolex. Such a matrix is, however, afforded by the numerous anastomosing branches and the two irregular rings and their connectives, seen in the rosette extremity.

These facts, with other considerations previously given, justify the homologizing of the scolex of the merozoic cestode with the rosette of *Gyrocotyle*, a posteriorly situated organ of attachment. This conclusion implies a functional reversal of the nervous system of the ancestral flatworm in the course of its development into a merozoic cestode. The greatest mass of nervous tissue, cephalized in the primitive flatworm, comes to lie in the posterior region of attachment of the cestode. The anterior

commissure disappears and the ring grows weak with the assumption of the sessile habit and the disappearance of sense-organs; while the posterior commissure develops with the increase in efficiency and complexity of the organ of attachment.

The orientation of cestodes here suggested has been advanced by several investigators, on more or less substantial grounds, from Perrier to the present day. This contention has been based for the most part on embryological evidence, especially with reference to the hexacanth onchospaeres so characteristic of cestodes. The well-established fact that the embryonic hooks are at the extremity of the cysticercus opposite to the one on which the organ of attachment is developed, and the further fact that the hook-bearing part of the onchospaere is directed forwards in the movement of the embryo, affords good ground for seriously questioning, if not altogether denying, the generally accepted identification of the scolex as "head." Barrois (1889) maintains that the anterior part of the scolex is that extremity which bears the embryonic hooks; that this part of the scolex gives rise to the first proglottis, which is therefore to be regarded as the "Kopftheil" of the primitive animal. Furthermore, the establishment of a zone of growth in the "neck" of the strobila suggests very strongly the penultimate "zone of growth" in annelids, with which the "neck" of the cestode is homologized if the scolex is recognized as posterior. A full presentation of the evidence in favor of this orientation, derived from embryological and comparative anatomical considerations such as the above, was given by Cohn (1907). He remarks that the present orientation of cestodes has been regarded as self-evident, incapable of proof; and proceeds to show that, aside from the habitus of the worm, there is no evidence in favor of this view. In his own words: "Meine These ist, dass dem Geschlechtstiere der Cestoden ein Kopf überhaupt fehlt, und sein Hinterende zu einem Haftorgane—dem Scolex—umgebildet ist." He regards the hook-bearing tail-like appendage of the cysticercoids as the homologue of the ancestral anterior extremity of the worm; this is discarded, leaving the posterior organ of attachment and the intermediate growing region of the body to constitute the adult cestode. "Wir haben in den Proliferationsfähigen Scolices also

Tiere, die ohne ein wahres Vorderende, d. h. einen Kopf zu besitzen, mit dem äussersten Hinterende sich an der Darmwand fixieren und mit ihren relativ vordersten Körperende frei in den Darm hineinhängen." He then proceeds to show that, first, the presence of a differentiated intermediate portion between the anterior and posterior segments of the body, secondly, the detachment of the posterior segment and its transformation into the sexually mature animal, and lastly, the location of the growth-zone in the penultimate region of the body, are conditions whose analogues can be readily found in other worms and also in echinoderms, bryozoans, etc. On the last and probably most important point, the location of the growth-zone, he sums up the evidence very briefly as follows:

"Ob wir also die normalen Wachstumserscheinungen, ob wir Regeneration oder die der autotomischen Teilung vorausgehenden Processe der Segmentvermehrung betrachten: überall finden wir dass sich die Wachstumzone beiden genannten Tieren an äussersten Hinterende des Körpers befindet. Bei der von mir vorgeschlagenen Orientierungen der Cestoden schaffen wir also in bezug auf die Wachstumsverhältnisse keinen Ausnahmefall sondern erhalten im Gegenteil erst so die Möglichkeit, das Wachstum der Cestoden durch Proliferation am Collum mit demjenigen anderer Vermes konform aufzufassen."

These considerations, arising from facts of comparative embryology and morphology of the invertebrates, taken together with those arising from a study of the morphology of the primitive genus *Gyrocotyle*, afford a warrant for serious question of the validity of the generally accepted orientation of cestodes. Furthermore, they constitute a more or less successful effort to take this question out of the realm of "self-evident" hypotheses incapable of either proof or disproof where, as Cohn pointed out, it has too long existed. Further embryological research, especially on such forms as *Amphilina* and *Gyrocotyle*, is greatly to be desired; from this field the final word on the question must be obtained. All the facts now at hand, however, seem to show that this decision will be in direct opposition to the generally accepted belief, and will place the organ of attachment in cestodes at the posterior extremity of the strobila.

F. SUMMARY.

1. The genus *Gyrocotyle* is composed of the following species: *G. rugosa*, *G. urna*, *G. nigrosetosa*, *G. fimbriata*. These are distinguished on the basis of the following specific characteristics:

- (1) Character of folds of terminal rosette.
- (2) The ratio between the distance from the opening of the uterus to the tip of the acetabulum, and the distance from the opening of the uterus to the level of the opening of the penis.
- (3) Character of lateral frills.
- (4) Presence and distribution of spines.
- (5) Size of tail-rosette.
- (6) Presence of hooked embryo in uterine eggs.
- (7) Presence of an eversible cirrus, adapted to self-impregnation.
- (8) Spinules lining ejaculatory duct.
- (9) Operculated uterine eggs.

2. The normal habitat of the sexually mature individual is in the spiral valve of the intestine of some species of the family Chimaeridae. Reported occurrences of *G. rugosa* in bivalve molluscs are probably accidental. Nothing is known of intermediate host or life-cycle of the parasite.

3. The functional orientation of *Gyrocotyle fimbriata* directs the acetabulum anteriorly, the rosette posteriorly. This is in agreement with Wagener's observations on the living *G. urna*, but in exact opposition to Lönnberg's observations on the same form. The worm is capable of definitely directed locomotion and is very active under favorable conditions. The exploring function of the acetabulum is strongly in evidence. The posterior rosette functions strictly as an organ of attachment. The acetabulum never functions as an organ of attachment.

4. This functional orientation is borne out by evidence from the structure of the central nervous system and by the presence on the margin of invagination of the acetabulum of a pair each of sensory pits and sensory papillae, abundantly innervated by heavy branches from the central nervous system.

5. The acetabular portion of the nervous system is developed in connection with the acetabular sense organs and with the power of locomotion in a definite direction. It corresponds to the "brain" of Turbellaria and to the anterior ganglionic commissure in Trematoda.

6. The rosette portion of the nervous system is developed in connection with the development of a powerful posterior organ of attachment, and is comparable to the posterior ring-commis- sure in the posterior sucker of a heterocotylean trematode.

7. The rosette of *Gyrocotyle* is in structure and function a true scolex, and corresponds to that organ in merozoic cestodes. This correspondence is strikingly shown in a comparison of the nervous system of the rosette of *Gyrocotyle* and that of the scolex of the merozoic cestodes.

8. On the basis of this evidence from comparative morphology and of other evidence previously adduced from the embryology of merozoic cestodes, it is proposed to regard the cestode scolex as a posteriorly situated organ of attachment, the "neck" or growing region as the antepenult region corresponding to the antepenult segment in annelids, and the proglottis as the intermediate region of the body. The anterior extremity has completely disappeared, according to this view.

9. The limiting-membrane in *Gyrocotyle* consists of a surface layer, composed of delicate fibres in a homogeneous matrix, and immediately beneath this a layer of transverse and a layer of longitudinal muscle fibres, non-nucleated. These are connected by fine processes with a layer of large cells lying in the parenchyma of the body, the subcuticular cells. Some at least of these cells are to be regarded as myoblasts of the cuticular musculature. There is no ground for regarding them as sunken epidermal cells. There is no trace in any of the tissues of the body of an epithelial layer of cells. The lining of the genital ducts is a meshwork of fibres in a homogeneous matrix, with nuclei scattered through it. This passes by gradual transition into the non-nucleated condition described for the limiting membrane of the body.

10. The muscle fibres of *Gyrocotyle* are all nucleated except those of the cuticular musculature. The latter are attached by

delicate processes to deeper-lying myoblasts (in the subcuticular layer).

11. The processes of cell-division in the maturation of the ovum are mitotic. A large "nucleolus" is formed within the nucleus and extruded into the cytoplasm. This process can easily be mistaken for an amitotic figure.

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LITERATURE CITED.

Barrois, J.

1889. Une nouvelle conception de l'organisme Cestode. *Rev. Biol. Nord France*, 2, 18-23, 199.

Benham, W. B.

1891. The *Platyhelmia*, *Mesozoa* and *Nemertini*. In *Lankester's Treatise on Zoology*, part IV, 1-204, with figs.

Blochmann, F.

1896. Die Epithelfrage bei Cestoden und Trematoden. Vortrag gehalten auf der VI. Jahresversammlung der deutschen zoologischen Gesellschaft zu Bonn. 16 pp., 2 pls. Hamburg.

Blumberg, C.

1877. Ein Beitrag zur Anatomie der *Taenia plicata*, *T. perfoliata*, und *T. mamillata*. *Arch. f. wiss. u. prakt. Thierhlkde*, 3, 33-44. pl. 1, figs. 1, 2.

Braun, M.

1889. *Gyrocotyle*, *Amphiptyches* und Verwandte. Zusammenfassender Bericht. *Centrbl. Bakter.*, 6, 436-441.

- 1894-1900. Cestodes. In *Bronn's Klassen und Ordnungen des Thierreichs*, 4, I b, pp. 927-1731, pls. 35-59.

Child, C. M.

1907. Studies on the relation between amitosis and mitosis. IV and V. *Biol. Bull.*, 13, 165-184, 19 figs.

Cohn, L.

1898. Untersuchungen über das centrale Nervensystem des Cestoden. *Zool. Jahrb. Anat.*, 12, 89-160, pls. 6-9, text figs. A-J.

1907. Die Orientierung der Cestoden. *Zool. Anz.*, 32, 51-56.

Dean, B.

1906. Chimaeroid Fishes and their development. 194 pp., 11 pls., 144 text figs. Carnegie Institution of Washington.

Diesing, C. M.

1850. *Systema Helminthum*. I; xiii, 679 pp. Vindobonae.

1855. Sechzehn Gattungen von Binnenwürmern und ihre Arten. *Denkschr. d. k. Akad. d. Wiss. Wien, Math.-naturw. Cl.*, 9, 171-185, pls. 1-6.

1858. Revision der Myzhelminthen. Abtheilung Trematoden. Sitzb. k. Akad. d. Wiss. Wien, Math.-naturw. Cl., 32, 207-390, 2 pls.
1859. Revision der Myzhelminthen. Abtheilung Bdellideen. *Ibid.* 33, 473-513.
1859. Nachträge und Verbesserungen zur Revision der Myzhelminthen. *Ibid.*, 35, 421-454.

Goto, S.

1891. *Diplozoon nipponicum* n.sp. Journ. Coll. Sci. Imp. Univ. Japan, 4, 151-192, pls. 21-23.

Grube, E.

1855. Bemerkungen über einige Helminthen und Meerwürmer. Arch. f. Naturg., 21, I, 137-158, pls. 6, 7.

Haswell, W. A.

1902. On a *Gyrocotyle* from *Chimaera ogilbyi*, and on *Gyrocotyle* in general. Proc. Linn. Soc., N. S. Wales, 1902, I, 48-54, pl. 7.

Hungerbühler, M.

1910. Studien an *Gyrocotyle* und Cestoden. Ergebnisse einer von L. Schultze ausgeführten zoologischen Forschungsreise in Südafrika. Inaug. Diss., Basel. 26 pp., 2 pls. Also in Jenais. Denkschr., 16, 3 Lief.

Kofoid, C. A., and Watson, Edna E.

1910. On the Orientation of *Gyrocotyle* and of the Cestode strobila. Advance print from Proc. Seventh Intern. Zool. Congr., 1907, 5 pp., 3 figs.

Lang, A.

1881. Untersuchungen zur vergleichenden Anatomie und Histologie des Nervensystems der Plathelminthen. IV. Nervensystem der Tricladen. Mt. Stat. Neapel, 3, 1-53, pls. 5, 6.
1891. Text-book of Comparative Anatomy, trans. by H. M. and M. Bernard, 1, pp. 133-176; figs. 102-120.

Lay, G. T., and Bennet, E. T.

1839. "Fishes" in Zoology of Captain Beechey's voyage. Bohn, London, 1839.

Linton, E.

1891. Notes on Entozoa of marine fishes of New England with descriptions of several new species. Part II. Rep. U. S. Fish Comm., 1887, 719-899, pls. 1-15.

Lönnberg, E.

- 1890a. Helminthologische Beobachtungen von der Westküste Norwegens. Cestoden. Bih. Svenska Ak., 16, IV, 5, 1-47.

- 1890b. Ueber *Amphiptyches* Wag. oder *Gyrocotyle urna* (Grube et Wagener) Diesing Verh. Biol. Ver. Stockholm, 3, 55-61.
- 1891. Anatomische Studien über Skandinavische Cestoden. Svenska Ak. Handl., N. F. 24, VI, 1-109, pls. 1-3, 47 figs.
- 1897. Beiträge zur Phylogenie der parasitischen Plathelminthen. Centrbl. Bakter. 22, I, 674-684, 725-731, figs. 1-4.

Looss, A.

- 1894. Die Distomen unserer Fische und Frosche. Neue Untersuchungen über Bau und Entwicklung des Distomen Körpers. Zoologica, 6, Heft. 16, 1-296, 9 pls.

Monticelli, F. S.

- 1888. Saggio di una morfologia dei trematodi. Tese per ottenere la privata docenza in Zoologia nella R. Università di Napoli. viii, 130 pp., ind. 1 p.
- 1889a. Sul sistema nervosa dell' *Amphiptyches urna* Grube et Wagener. Zool. Anz., 12, 142-144.
- 1889b. *Gyrocotyle* Diesing, *Amphiptyches* Grube et Wagener. Atti Acc. Lincei Rendic. cl. sci. fis. mat. e nat. (4), 5, 228-230.
- 1889c. Notes on some entozoa in the collection of the British Museum. P. Zool. Soc. London, 1889, 321-325, pl. 33.
- 1890. Alcuni considerazioni biologiche sul genere *Gyrocotyle*. Atti Soc. Ital. di Sci. Nat., 32, 327-329.
- 1892. Appunti sui Cestodaria. Atti R. Accad. Sci. fis. mat. Napoli (2), 5, 67-78, 4 figs.

Niemiec, J.

- 1886. Untersuchungen über das Nervensystem der Cestoden. Arb. Zool. Inst. Wien, 7, 1-60, pls. 1, 2.

Olsson, P.

- 1896. Sur *Chimaera monstrosa* et ses parasites. Mém. Soc. Zool. France, 9, 499-512, figs. 1-9.

Pintner, Th.

- 1880. Untersuchungen über den Bau des Bandwurmkörpers mit besonderer Berücksichtigung der Tetrabothrien und Tetrahyrnchen. Arb. Zool. Inst. Wien, 3, 163-242, 5 pls.

Pratt, H. S.

- 1909. The cuticula and subcuticula of trematodes and cestodes. Amer. Nat., 43, 705-729.

Salensky, W.

1874. Ueber den Bau und die Entwicklungsgeschichte der *Amphilina* G. Wagener (*Monostomum foliaceum* Rud.). Z. wiss. Zool., 24, 291-342, pls. 28-32.

Schiefferdecker, P.

1874. Beiträge zu Kenntniss des feineren Baues der Taenien. Jena. Zeitschr. f. Naturw. 8, 459-487, pl. 16.

Spencer, W. B.

1889. Anatomy of *Amphiptyches urna* Grube et Wagener. Tr. R. Soc. Victoria, 1, 138-151, pls. 11-13.

Tower, W. L.

1900. Nervous system of the cestode *Moniezia expansa*. Zool. Jahrb. Anat., 13, 359-384, pls. 21-26.

van Beneden, P. J., et Hesse, C. E.

1864. Recherches sur les bdellodes ou hirudinées et les trématodes marins. Mém. Ac. Belgique, 38, Mém. I, 1-142, pls. 1-13.

Wagener, G.

1852. Ueber einen neuen in der *Chimaera monstrosa* gefundenen Eingeweidewurm. Arch. f. Anat. und Physiol., 1852, 543-554, pls. 14, 15.
1858. Enthelminthica No. V. Ueber *Amphilina foliacea* (*Monostomum foliaceum* Rud.) *Gyrocotyle* Diesing und *Amphiptyches* Gr. W. Arch. f. Natürg., 24, I, 244-249, 1 pl.

Will, H.

1893. Anatomie von *Caryophyllaeus mutabilis* Rud., ein Beitrag zur Kenntniss der Cestoden. Z. wiss. Zool., 56, 1-39, pls. 1, 2, 2 figs. in text.

DESCRIPTION OF PLATES.

All figures are drawn with a Zeiss camera lucida, unless otherwise stated.

PLATE 33.

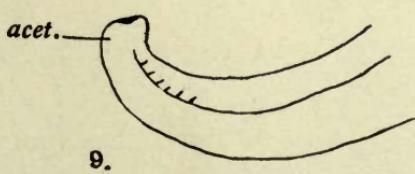
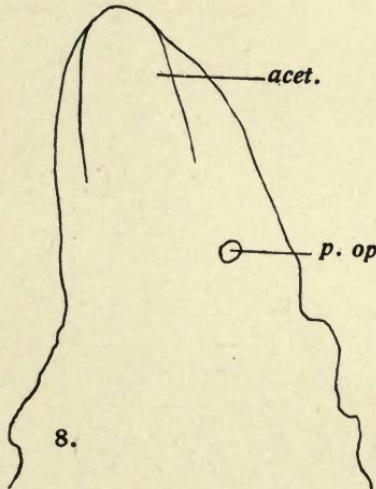
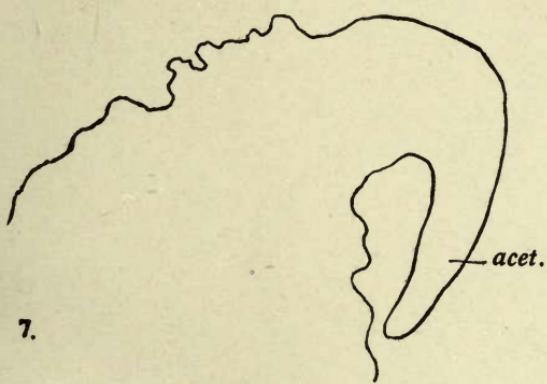
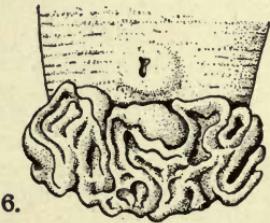
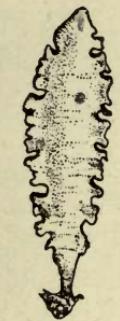
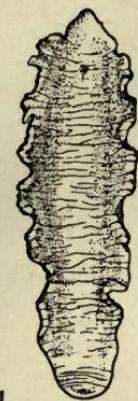
Figs. 1-4. Changes in form of living *Gyrocotyle*, as seen by Lönnberg (1891, Taf. III, figs. 34, 35, 36, 37). Fig. 1, the *Ligula*-like form; fig. 2, rosette extended into long tube; figs. 3 and 4, form ordinarily assumed by animal.

Figs. 5 and 6, Diesing's figures of *Gyrocotyle rugosa*. (Diesing 1855, Taf. 1, figs. 17, 20.)

Figs. 7, 8, 9. Sketches of the acetabulum of a living specimen. Figs. 7, 9, extended; fig. 8, contracted.

acet.—acetabulum.

p. op.—penis opening.





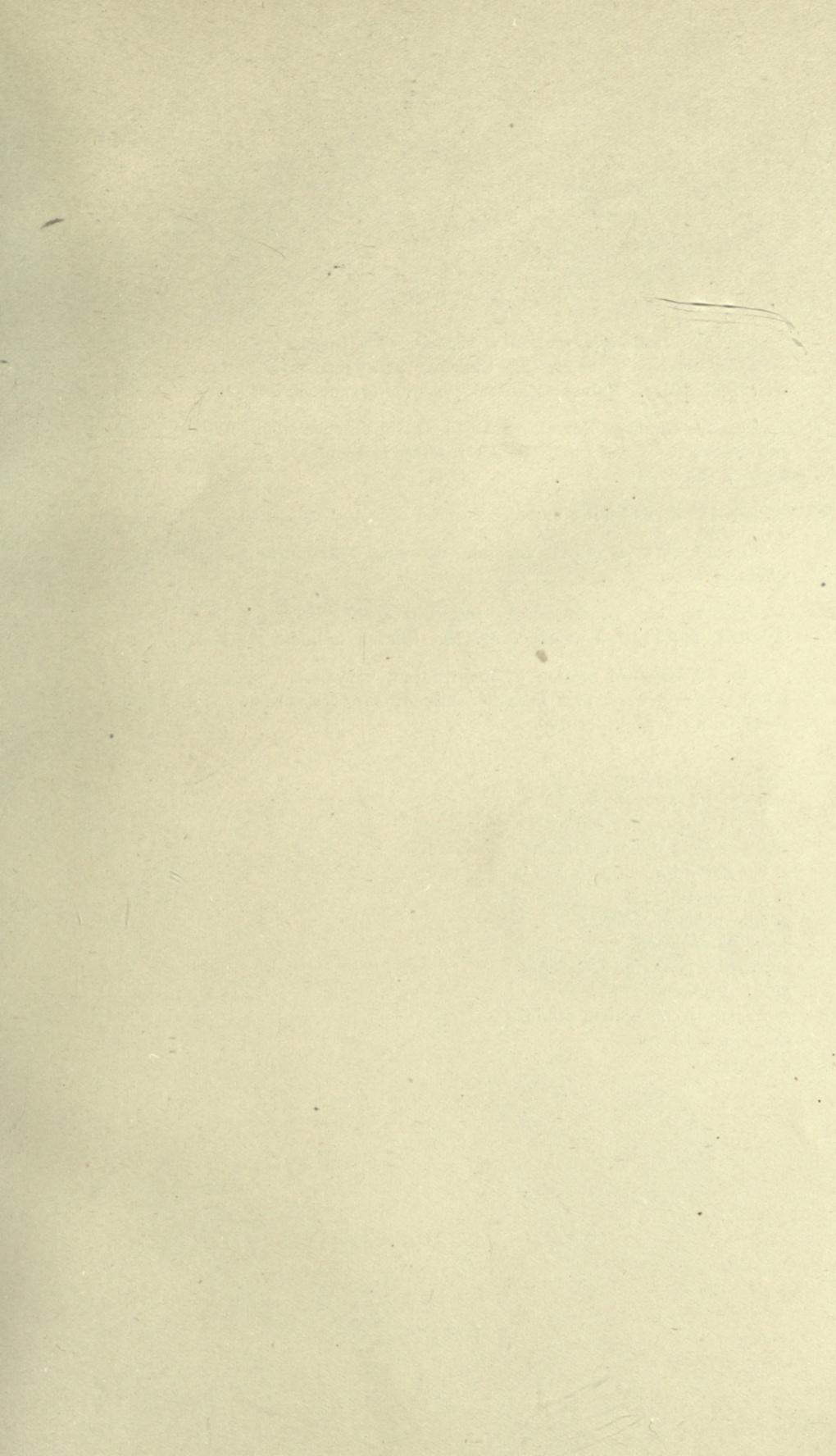


PLATE 34.

Fig. 10. *Gyrocotyle fimbriata*, ventral. Flattened, stained in borax-carmine, cleared in cedar-oil. Showing arrangement of spines at posterior extremity. Spines at anterior extremity not shown. $\times 4$.

Fig. 11. *G. urna*, dorsal. Stained flattened specimen. Showing size and character of folds of posterior rosette, and collar of spines about the neck of the rosette. $\times 4$.

Fig. 12. *G. fimbriata*, dorsal. Stained flattened specimen. $\times 4$.

Fig. 13. *G. urna* (var.), ventral. Showing distribution of spines over whole surface. $\times 7$.

Figs. 14, 15. *G. fimbriata*. Showing canal-opening, with proboscis inverted, fig. 14, and everted, fig. 15. Sketch without camera.

Fig. 16. Sagittal section of longitudinal nerve-stem, showing sheath-cells, branch-nerves, and ganglion-cells of the first order. Iron haematoxylin-erythrosin. $\times 100$.

acet.—acetabulum.

can. op.—canal opening.

gang. 1st.—ganglion cell of the first order.

gen. notch—genital notch.

n. b.—nerve branch.

n. fib.—nerve fibre.

p. op.—penis opening.

par.—parenchyma.

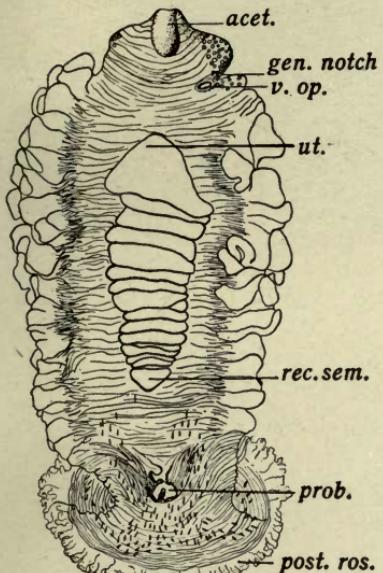
post. ros.—posterior rosette.

prob.—proboscis.

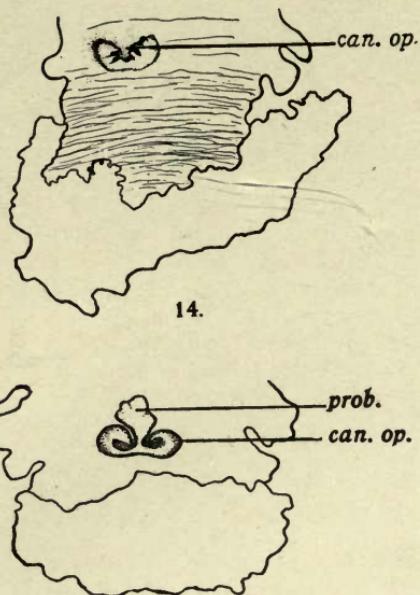
rec. sem.—receptaculum seminis.

sh. c.—sheath cell.

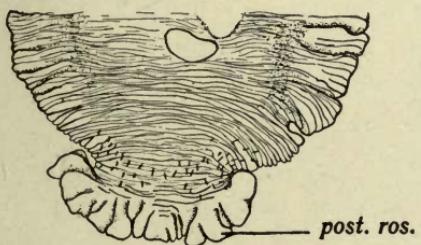
ut.—uterus.



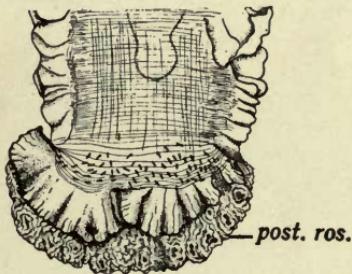
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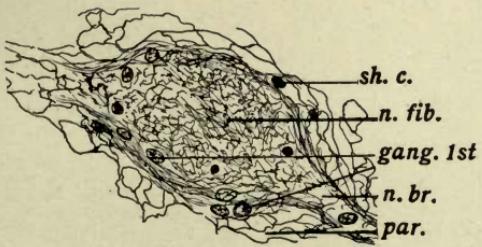
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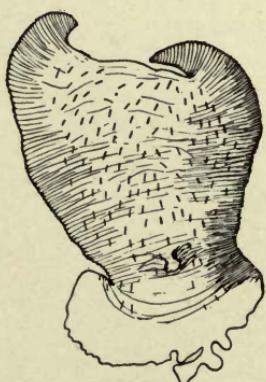
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PLATE 35.

Fig. 17. *Gyrocotyle fimbriata*. Diagram of the nervous system of the posterior extremity. From Kofoid and Watson (1910, fig. 3).

Fig. 18. Diagram of the arrangement of muscle-layers in the saggital section.

Fig. 19. Diagram showing track made by living specimen across dish. Distance traversed, about 14 cm.; four contractions.

Fig. 20. Sketch of network of excretory canals in the lateral fold as seen in a living specimen. Zeiss-Greenough binocular.

Fig. 21. Diagram, reproductive system, typical heterocotylean trematode. (After Benham, 1891, p. 51.)

cut.—cuticle.

cut. trans.—cuticular transverse muscle.

cut. long.—cuticular longitudinal muscles.

dist. r. comm.—distal ring commissure.

ex. can.—excretory canal.

in. long.—inner longitudinal muscle.

in. trans.—inner transverse muscle.

lat. f.—lateral fold.

lat. long. conn.—lateral longitudinal connective.

marg. ex. sin.—marginal excretory sinus.

med. long. conn.—median longitudinal connective.

out. long.—outer longitudinal muscle.

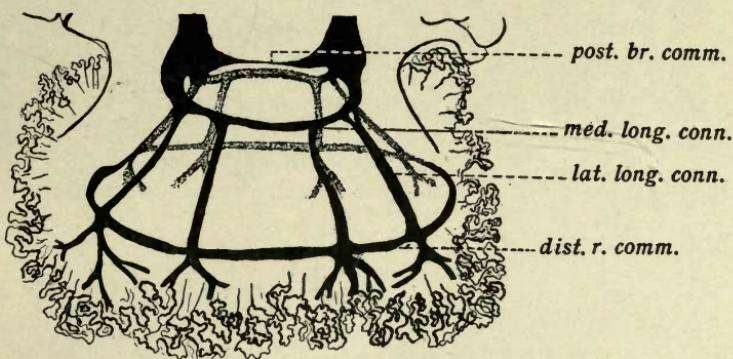
out. trans.—outer transverse muscle.

post. br. comm.—posterior bridge commissure.

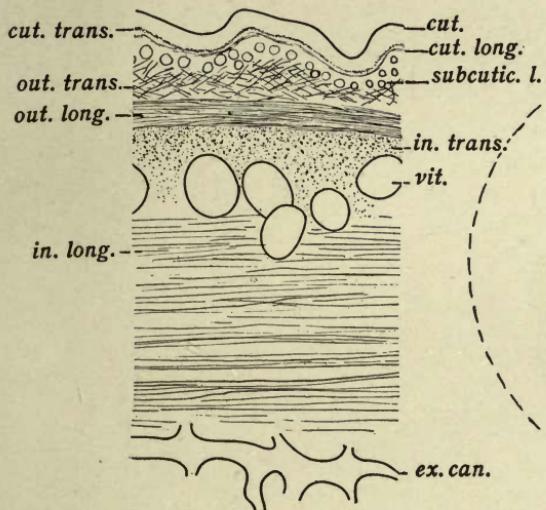
subcutic. l.—subcuticular layer.

vit.—vitellaria.

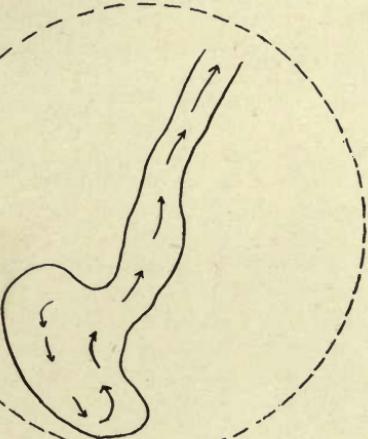
v. op.—vaginal opening.



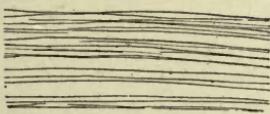
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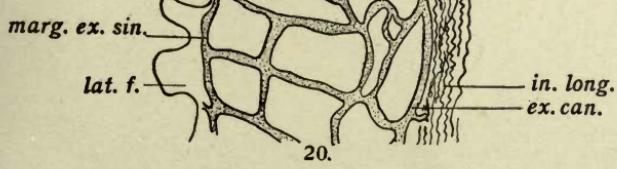
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20.



21.



PLATE 36.

Figs. 22, 23. *Gyrocotyle fimbriata*, anterior extremity, ventral and dorsal. Showing sensory pits and arrangement of spines. From preserved specimen. $\times 13$.

Fig. 24. *G. urna* (var.). Sketch from life. Lateral view, expanded. Showing spines, lateral fold and posterior rosette.

Fig. 25. *G. fimbriata*. Dorsal half of sagittal section of tip of acetabulum, showing sensory pit. Borax-carmine, Lyon's blue. $\times 430$.

Fig. 26. *G. fimbriata*. Sketch, life, acetabular extremity. Showing anterior excretory ring and deeper-lying ciliated canals.

Fig. 27. *G. fimbriata*. Sagittal section just laterad of the acetabulum. Showing anterior longitudinal nerve stem, with branches and anterior ganglionic knot. No histological detail; position of giant-cells within ganglion knot marked by small circles.

- acet. op.—acetabular opening.
ant. ex. r.—anterior excretory ring.
ant. gang. kn.—anterior ganglion knot.
ant. lat. n. st.—anterior lateral nerve stem.
cil.—cilia.
cut.—cuticula.
ex. can.—excretory canal.
gen. notch—genital notch.
lat. f.—lateral fold.
par. nuc.—parenchyma nucleus.
p. op.—penis opening.
post. ros.—posterior rosette.
sens. pit—sensory pit.
sp.—spine.
test.—testis.
ut. po.—uterine pore.
test. n.—testicular nerve.

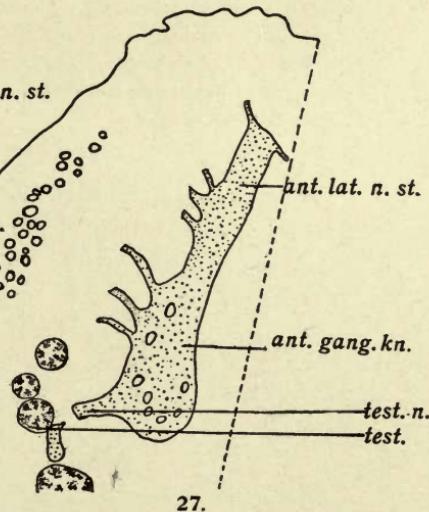
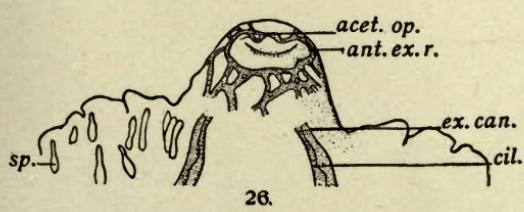
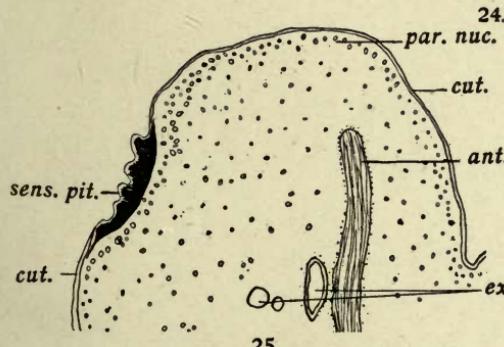
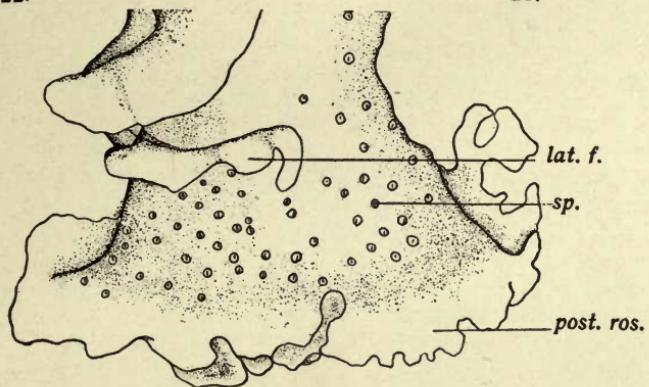
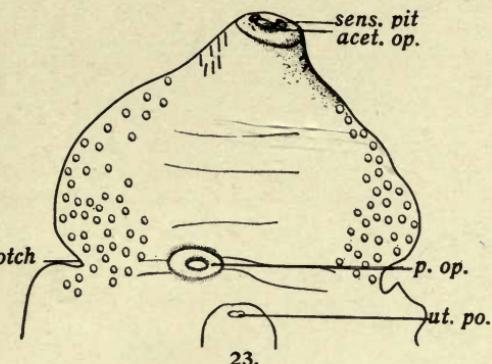
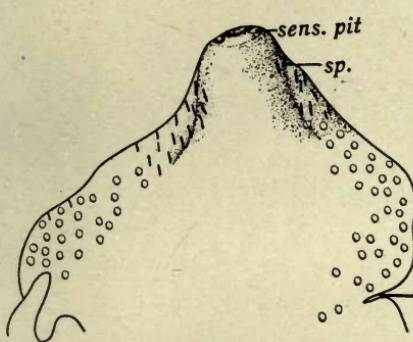




PLATE 37.

Figs. 28, 29. *Gyrocotyle fimbriata*. Spines, from acetabular group. Teased out. $\times 1000$.

Fig. 30. *G. fimbriata*. Spine, from neck of rosette. From specimen stained in borax-carmine and cleared in cedar-oil. Showing direction of spine and attachment of muscles. $\times 430$.

Fig. 31. *G. fimbriata*. Spine from neck of rosette. From same specimen as fig. 30. Drawn in situ. $\times 430$.

Fig. 32. Spines from margin of anterior end, in front of genital notch. Teased out. $\times 1000$.

Fig. 33. *G. fimbriata*, transverse section. Cuticula absent. Showing muscles of spine. $\times 430$. Iron haematoxylin.

Fig. 34. Same as fig. 33. Showing structure of socket of spine. $\times 1000$.

Fig. 35. Spine from neck of rosette. $\times 1000$.

musc. fib.—muscle fibre.

par. felt—parenchyma felt.

par. nuc.—parenchyma nucleus.

protr. m.—protractor muscle.

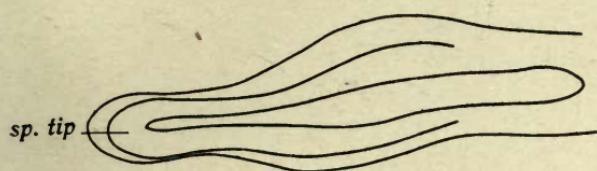
retr. m.—retractor muscle.

sp.—spine.

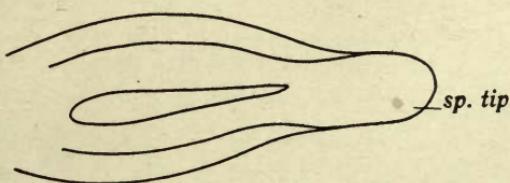
sp. base—spine base.

sp. sock.—spine socket.

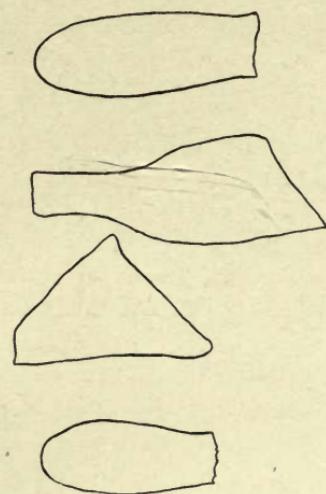
sp. tip—tip of spine.



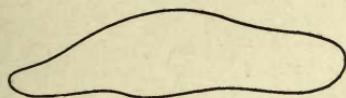
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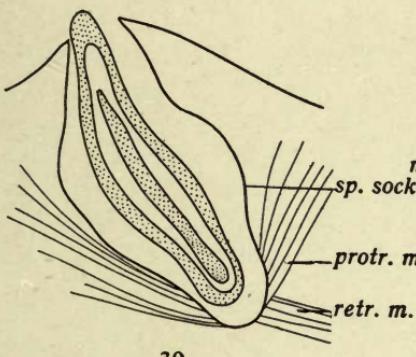
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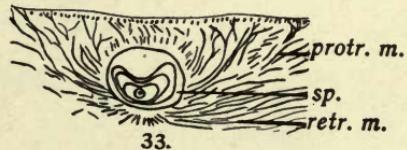
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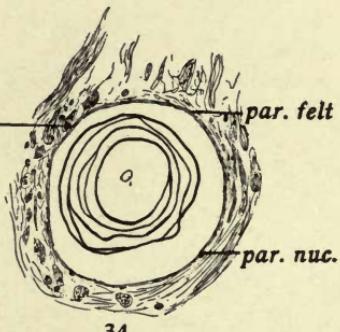
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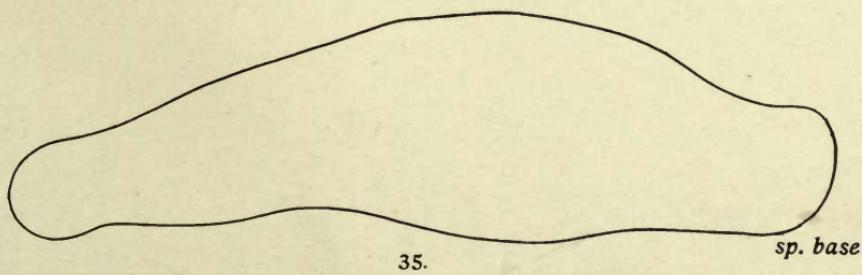
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34.



35.

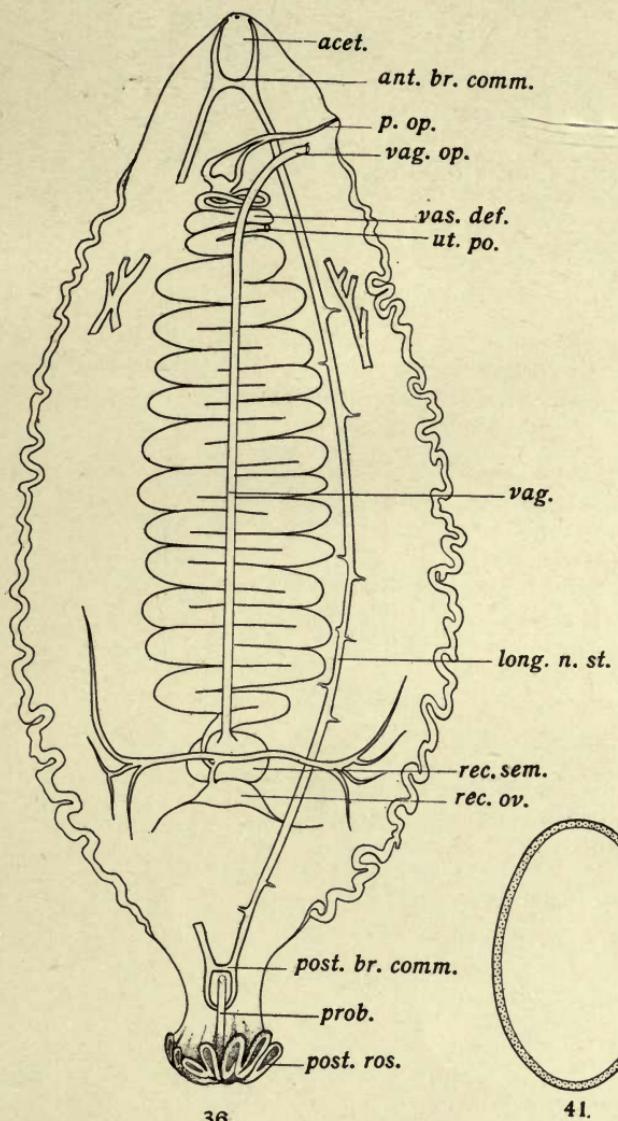


PLATE 38.

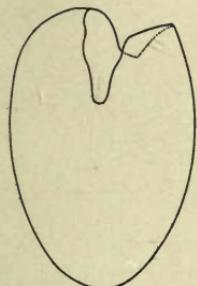
Fig. 36. *Gyrocotyle rugosa*, from Spencer (1889, pl. 1, fig. 1). To show size and character of lateral folds and posterior rosette and position of genital pores. $\times 1.5$, based on Spencer's reported magnification of 3 which is possibly an error.

Fig. 37-41. Eggs of *G. fimbriata*. Figs. 37-40, from decayed or macerated specimens; fig. 41, from living worm. $\times 500$.

- acet.*—acetabulum.
ant. br. comm.—anterior bridge commissure.
long. n. st.—longitudinal nerve stem.
operc.—operculum.
p. op.—penis opening.
post. br. comm.—posterior bridge commissure.
post. ros.—posterior rosette.
prob.—proboscis.
rec. ov.—receptaculum ovorum.
rec. sem.—receptaculum seminis.
ut. po.—uterine pore.
vag.—vagina.
vag. op.—vaginal opening.
vas def.—vas deferens.

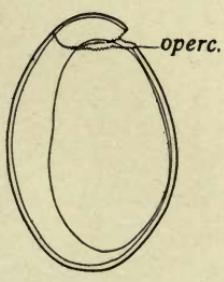
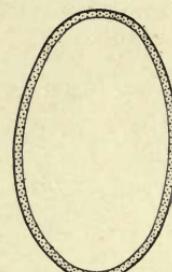


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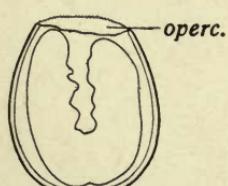


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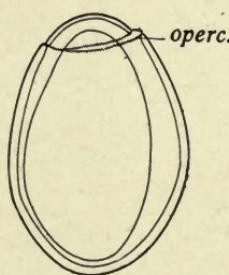
41.



38.



39.



40.



PLATE 39.

Fig. 42. *Gyrocotyle fimbriata*, dorsal. Specimen flattened, stained in borax-carmine; cleared in cedar-oil. $\times 13$.

acet.—acetabulum.

acet. op.—acetabular opening.

ant. br. comm.—anterior bridge commissure.

ant. lat. n. st.—anterior lateral nerve stem.

gen. notch—genital notch.

lat. f.—lateral fold.

long. n. st.—longitudinal nerve stem.

ovar.—ovary.

p. op.—penis opening.

pen. pap.—penis papilla.

post. br. comm.—posterior bridge commissure.

post. gang. kn.—posterior ganglion knot.

post. ros.—posterior rosette.

prox. r. comm.—proximal ring commissure.

rec. sem.—receptaculum seminis.

ros. n.—“neck” of rosette.

sh. gl.—shell gland.

ut. po.—uterine pore.

vag.—vagina.

vas def.—vas deferens.

vit. d.—vitelline duct.

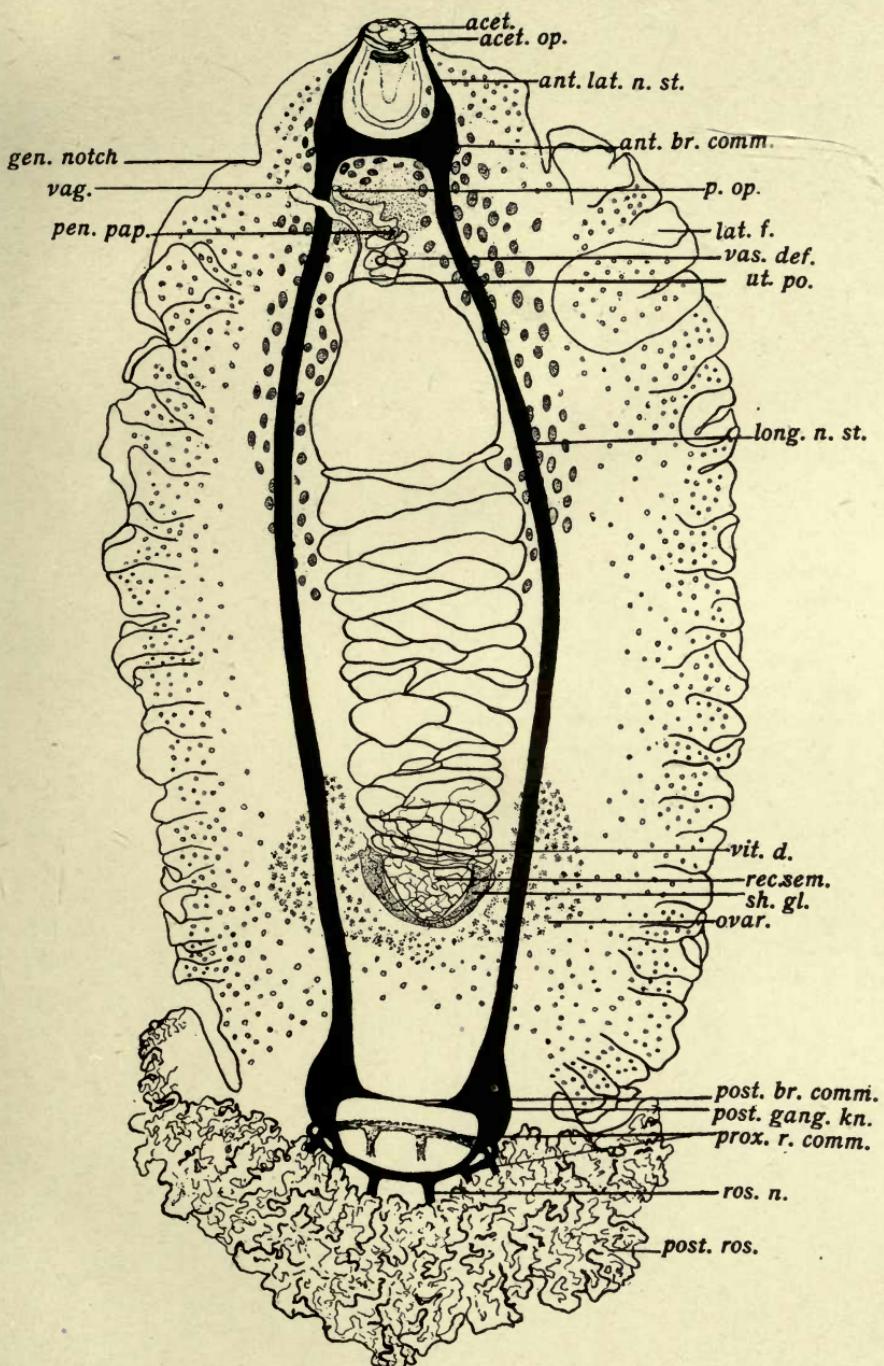




PLATE 40.

Fig. 43. *G. fimbriata*, sagittal section. To show structure of acetabulum and attachment of inner longitudinal muscles. Borax-carmine, Lyon's blue. $\times 100$.

Fig. 44. Diagram, showing musculature of canal opening.

Fig. 45. Same as fig. 43, showing detail of acetabular sphincter. $\times 430$.

acet. lum.—acetabular lumen.

acet. op.—acetabular opening.

acet. sphinc.—acetabular sphincter.

ant. br. comm.—anterior bridge commissure.

ant. lat. n. st.—anterior lateral nerve stem.

can. op.—canal opening.

in. long.—inner longitudinal muscle.

in. mer.—inner meridional muscle.

in. trans.—inner transverse muscle.

out. circ.—outer circular muscle.

out. long.—outer longitudinal muscle.

out. mer.—outer meridional muscle.

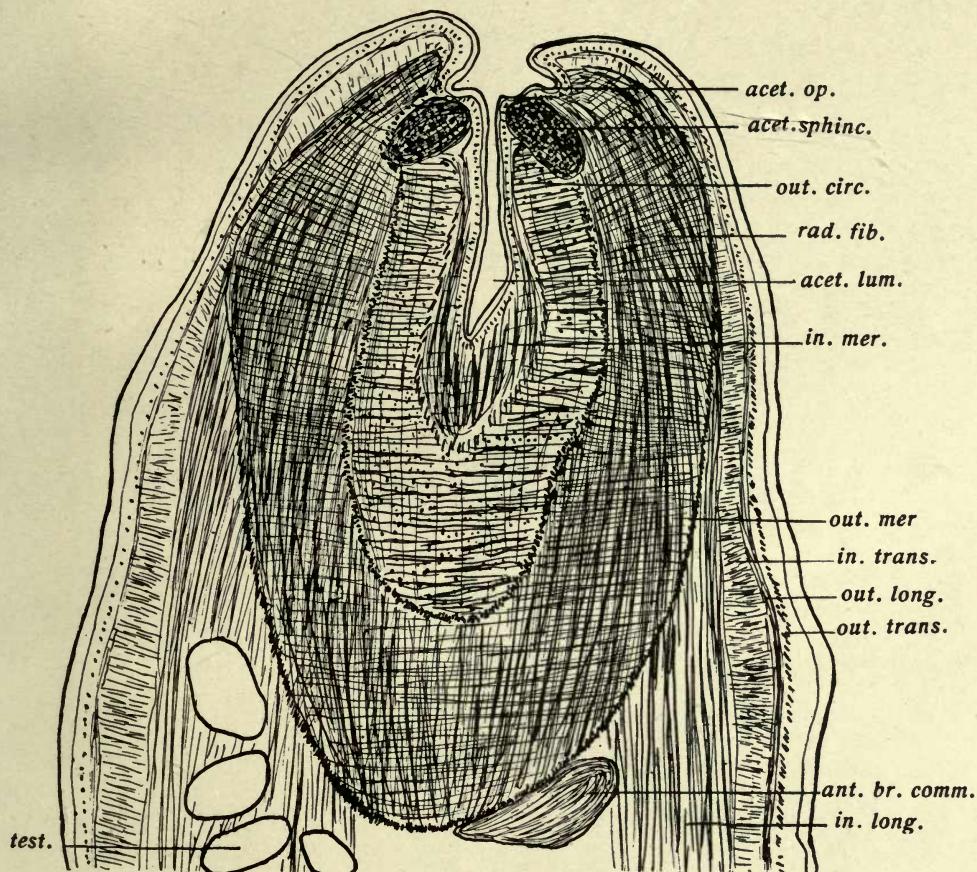
out. trans.—outer transverse muscle.

rad. fb.—radial fibre.

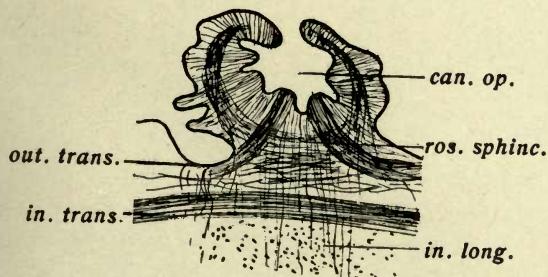
ros. sphinc.—rosette sphincter.

sphinc.—sphincter.

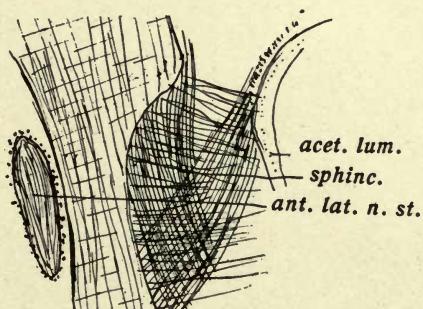
test.—testis.



43.



44.



45.



PLATE 41.

Fig. 46. *Gyrocotyle fimbriata*. Same specimen as fig. 42. Ventral. Showing vagina and vaginal opening, vesicula seminalis, penis-papilla and ejaculatory duct. $\times 100$.

Fig. 47. Egg from fifth coil of uterus. Showing single ovum surrounded by numerous yolk-cells. Delafield's haematoxylin. $\times 1000$.

Fig. 48. Same, tenth coil of uterus. Showing division of ovum and disintegration of yolk cells. Note disappearance of nuclei of yolk cells. $\times 1000$.

Fig. 49. Yolk cells in vitellarian follicle. Note reduction of cytoplasm and formation of yolk-platelets. $\times 1850$.

Fig. 50. Spermatozoa from receptaculum seminis, showing head, tail and acrosome. $\times 1850$.

Fig. 51. Ovum in afferent oviduct; note shadow of yolk nucleolus. $\times 1500$.

Figs. 52, 53, 54. Follicle of ovary. Showing syncytial ova and various stages in the formation and extrusion of the yolk-nucleolus. $\times 1500$.

cyt. r.—cytoplasmic rim.

ejac. duct—ejaculatory duct.

in. long.—inner longitudinal muscle.

ov.—ovum.

pen. pap.—penis papilla.

sptz.—spermatozoa.

ut.—uterus.

vag.—vagina.

vag. op.—vaginal opening.

vas def.—vas deferens.

yk. c.—yolk cell.

yk. gr.—yolk platelets.

yk. nucleo.—yolk nucleolus.

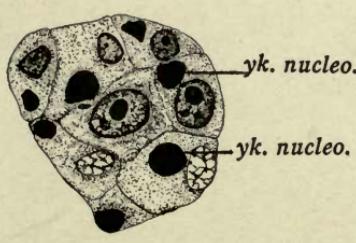
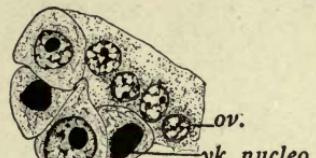
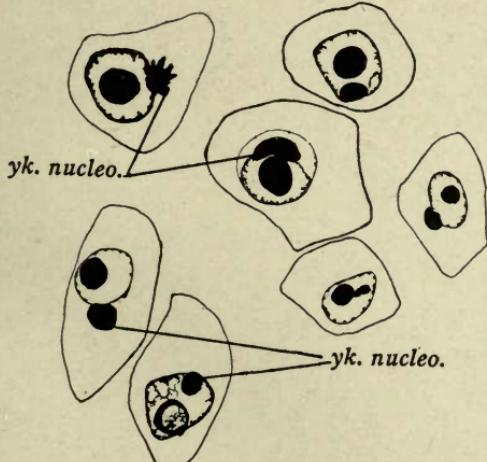
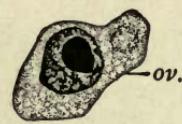
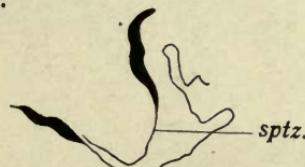
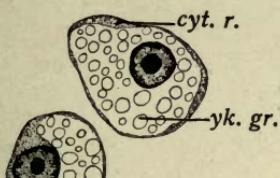
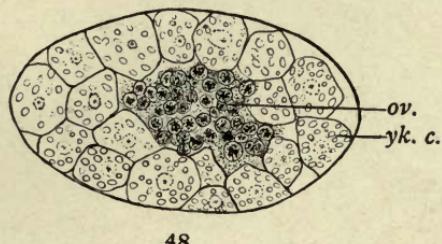
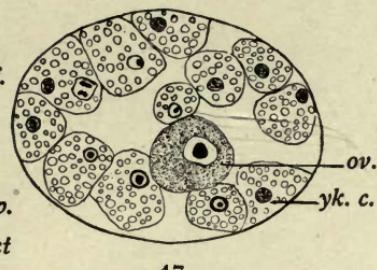
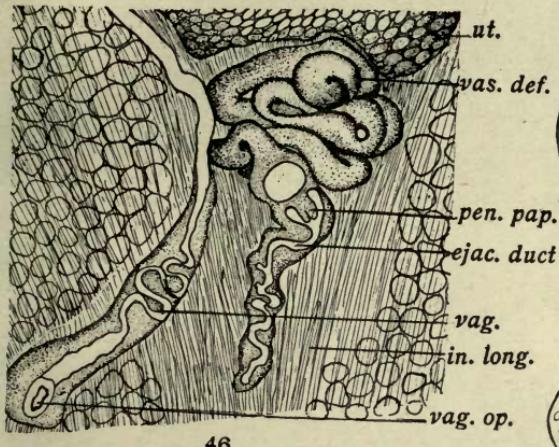




PLATE 42.

Fig. 55. *Gyrocotyle fimbriata*. Transverse section, showing cuticula and cuticular musculature. Iron haematoxylin. $\times 1500$.

Fig. 56. Showing structure of muscle fibres of the inner circular and inner longitudinal layers. $\times 1850$.

Fig. 57. Showing sagittal (upper) and outer transverse (lower) muscle cells. $\times 1850$.

Fig. 58. Frontal section of cuticula and cuticular musculature. Cut through a fold of body-covering, in the plane of the fibres of the cuticular musculature. $\times 1850$.

Fig. 59. Showing wall of receptaculum seminis, and undifferentiated nucleated muscle fibres lying in the parenchyma of which it is composed. $\times 1850$.

cut.—cuticula.

cut. long.—cuticular longitudinal muscle.

cut. trans.—cuticular transverse muscle.

ext. cut. l.—external cuticular layer.

in. long. fib.—inner longitudinal fibre.

in. trans.—inner transverse muscle.

in. trans. fib.—inner transverse fibre.

nuc.—nucleus.

out. long.—outer longitudinal muscle.

out. trans.—outer transverse muscle.

out. trans. fib.—outer transverse fibre.

par. felt—parenchyma felt.

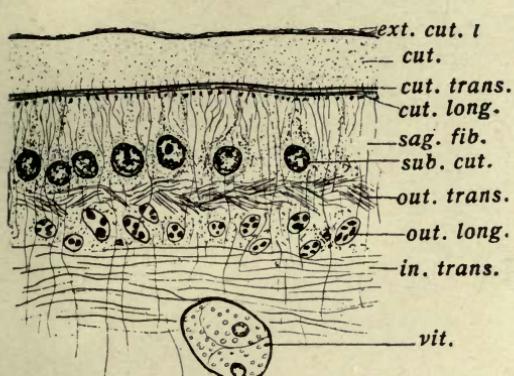
par. nu.—parenchyma nucleus.

sag. fib.—sagittal fibre.

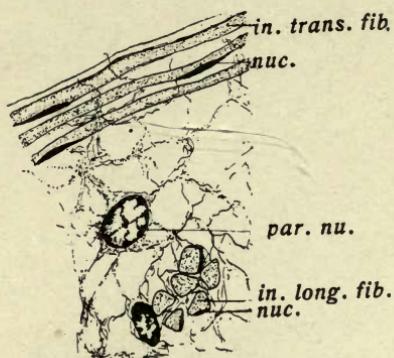
sub. cut.—subcuticula.

undif. musc. fib.—undifferentiated muscle fibre.

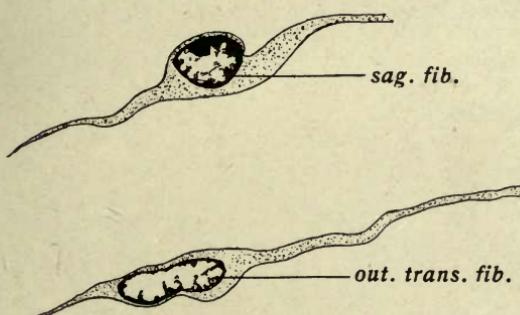
vit.—vitellaria.



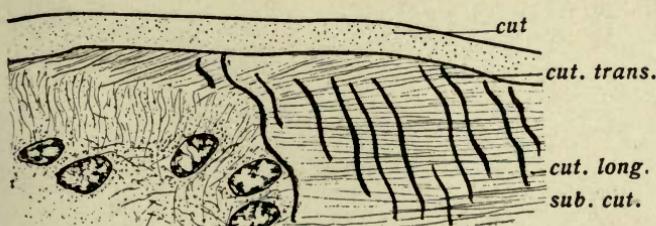
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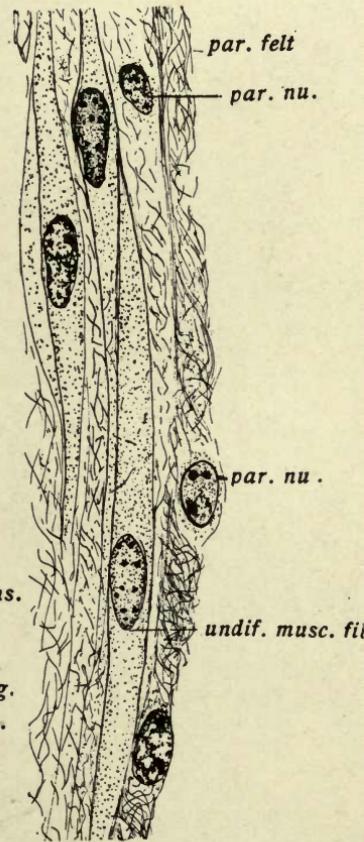
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58



59



PLATE 43.

Fig. 60. *Gyrocotyle fimbriata*. Transverse section through ciliated excretory canal. Showing circular muscle coat. Iron haematoxylin. $\times 1000$.

Fig. 61. Longitudinal section through ciliated excretory canal (taken at one side of attachment of cilia). Showing circular muscle coat. Iron haematoxylin. $\times 1000$.

Figs. 62, 63. Flame cells. $\times 1500$.

Fig. 64. Cells of prostate gland. $\times 1500$.

Fig. 65. Sagittal section through penis papilla and ejaculatory duct. $\times 100$.

can.—canal.

cil.—cilia.

circ. musc. l.—circular muscle layer.

ejac. duct—ejaculatory duct.

fl.—flame.

long. musc. l.—longitudinal muscle layer.

in. long.—inner longitudinal muscle.

par.—parenchyma.

par. nu.—parenchyma nucleus.

pen. pap.—penis papilla.

prost. d.—prostate duct.

prost. gl.—prostate gland.

rad. musc. f.—radial muscle fibre.

spnl.—spinule.

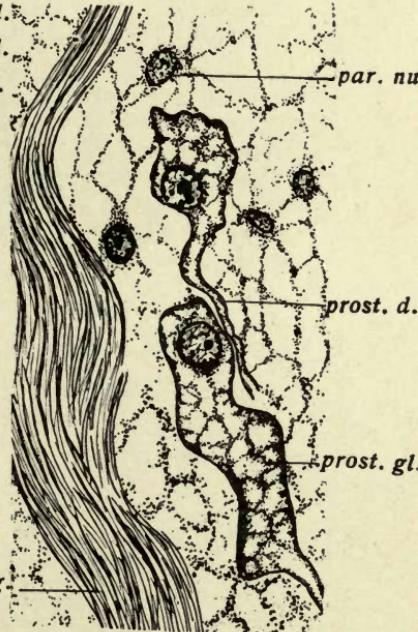
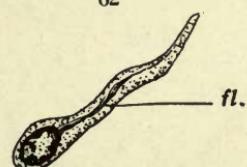
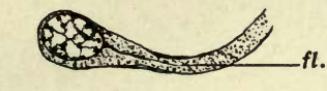
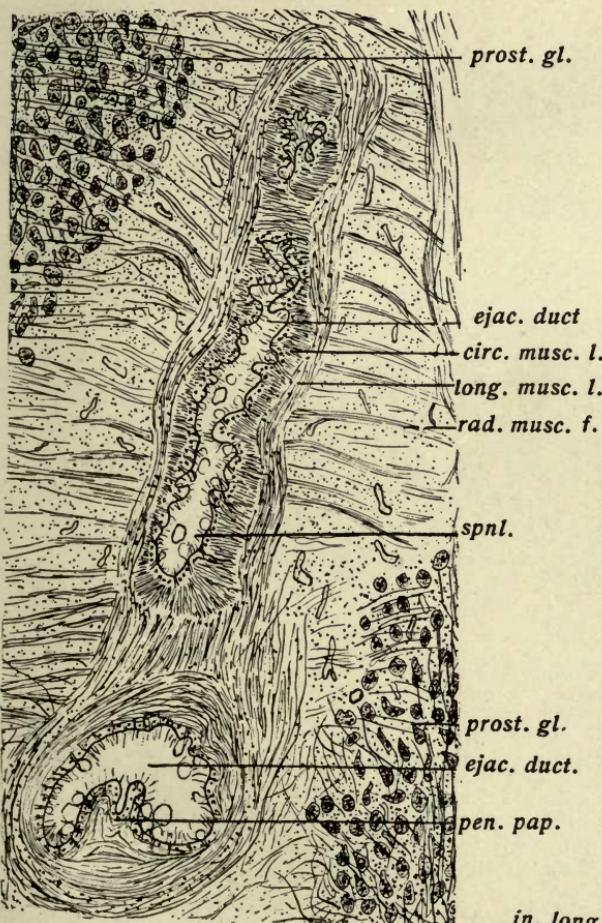
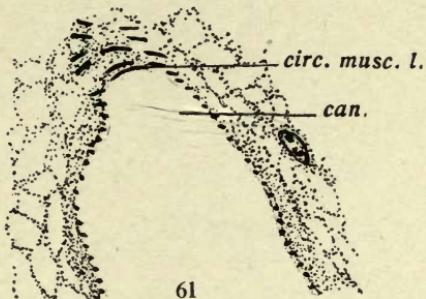
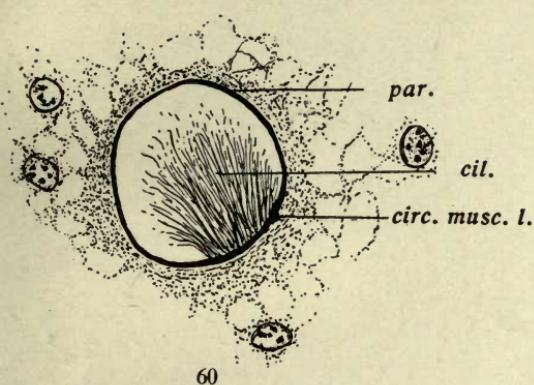




PLATE 44.

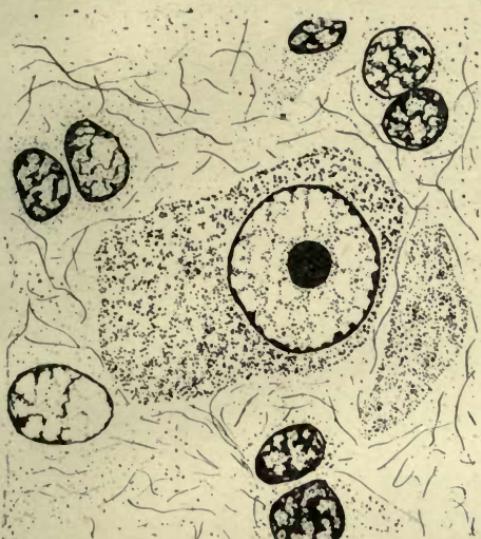
Fig. 66. *Gyrocotyle fimbriata*. From posterior ganglionic knot. Showing ganglion cells of first order and a ganglion cell of the second order ("giant cells"). $\times 800$.

Fig. 67. Cross section of longitudinal nerve stem, at region from which a branch to the ovary is given off. $\times 800$.

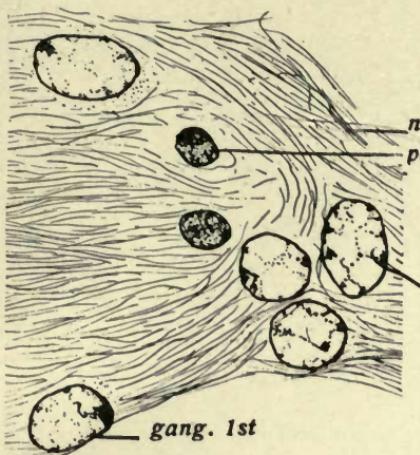
Fig. 68. Cells of shell-gland. $\times 1500$.

Fig. 69. Diagram of receptaculum seminis and the ducts which unite to form the uterus.

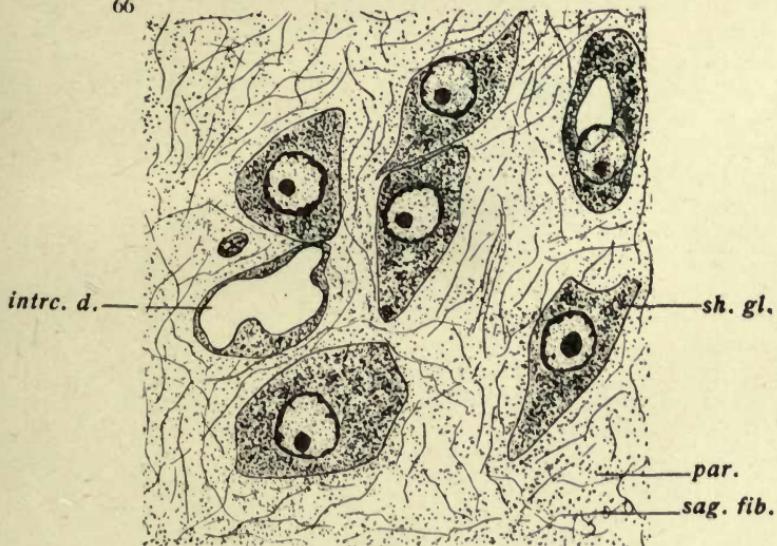
- duct. sem.*—ductus seminalis.
ef. vit. d.—efferent vitelline duct.
gang. 1st.—ganglion-cell of the first order.
intrac. d.—intracellular duct.
n. br.—branch nerve.
par.—parenchyma.
par. muc.—parenchyma nucleus.
rec. ovar.—receptaculum ovarium.
rec. sem.—receptaculum seminis.
sag. fib.—sagittal fibre.
sh. gl.—shell gland.
ut. c.—uterine coil.
vit. d.—vitelline duct.
yk. res.—yolk reservoir.



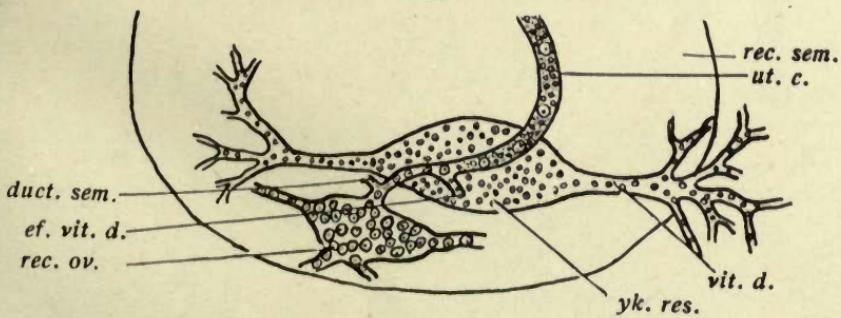
66



67



68



69



PLATE 45.

Figs. 70, 75. *Gyrocoyle fimbriata*. Sagittal section, nearly median. Diagrammatic. $\times 13$.

Figs. 71, 72, 73. Transverse sections, showing (71) emergence of ductus seminalis from receptaculum seminis; (73) fusion of the efferent vitelline duct with the efferent oviduct, which thus becomes the uterus. $\times 100$.

Fig. 74. Sagittal section through dorsal half of neck of funnel. Showing contrast between cuticula of funnel cavity and of the surface of the body. $\times 1000$.

acet.—acetabulum.

cut.—cuticula.

duct. sem.—ductus seminalis.

ef. ovd.—efferent oviduct.

ef. vit. d.—efferent vitelline duct.

ejac. duct—ejaculatory duct.

ex. can.—excretory canal.

in. long.—inner longitudinal.

lat. long. conn.—lateral longitudinal connective.

long. n. st.—longitudinal nerve stem.

mus. bd.—muscle bundle.

oot.—ootype.

ovar.; ov.—ovary.

post. ros.—posterior rosette.

pros. gl.—prostate gland.

rec. ovor.—receptaculum ovorum.

rec. sem.—receptaculum seminis.

subcutic. l.—subcuticular layer.

sh. gl.—shell gland.

test.—testis.

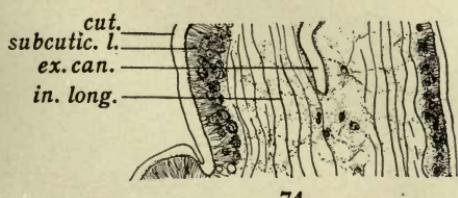
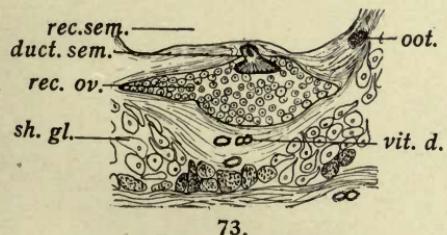
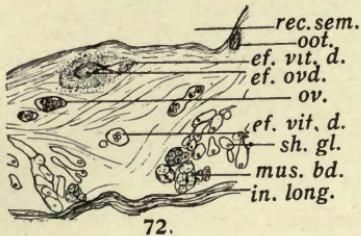
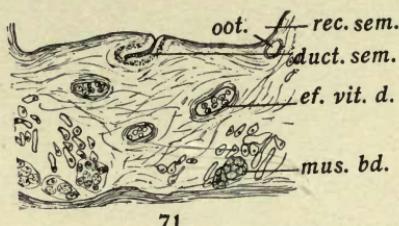
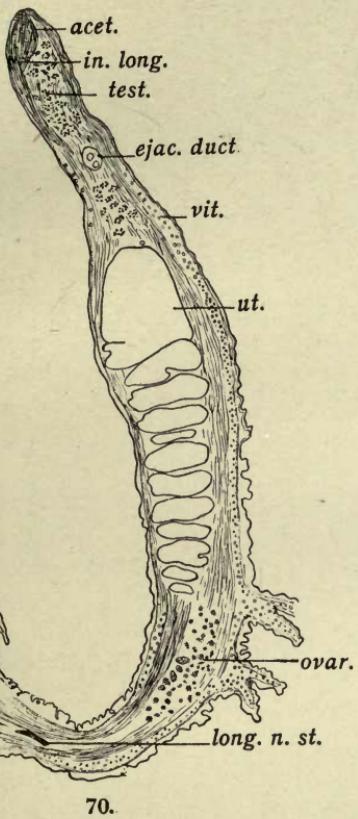
ut.—uterus.

ut. c.—uterine coil.

vag.—vagina.

vit.—vitellaria.

vit. d.—vitelline duct.



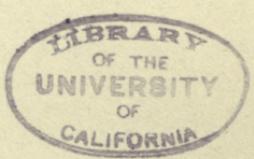


PLATE 46.

Fig. 76. *Gyrocotyle fimbriata*. Median sagittal section, posterior extremity. Showing funnel, canal, funnel-opening, canal-opening and sections of the ring commissures of the nervous system of the posterior extremity. $\times 100$.

Fig. 77. Same, to left of median. Reconstruction of five sections, showing lateral view of nervous system. Faint dotted lines indicate course of nerves as shown in the neighboring sections; heavy dotted lines indicate position of funnel with reference to the central nervous system. $\times 100$.

can. op.—canal opening.

ex. can.—excretory canal.

lat. anast.—lateral anastomosis.

lat. long. conn.—lateral longitudinal connective.

post. br. comm.—posterior bridge commissure.

post. gang. kn.—posterior ganglion knot.

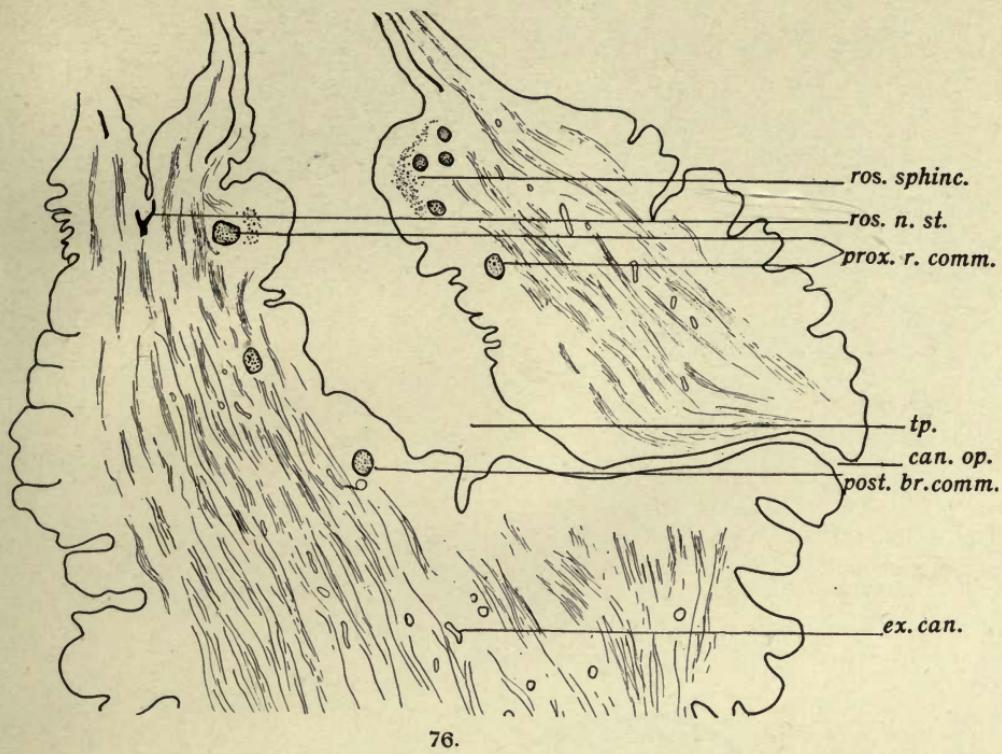
prox. r. comm.—proximal ring commissure.

ros. n. st.—rosette nerve stem.

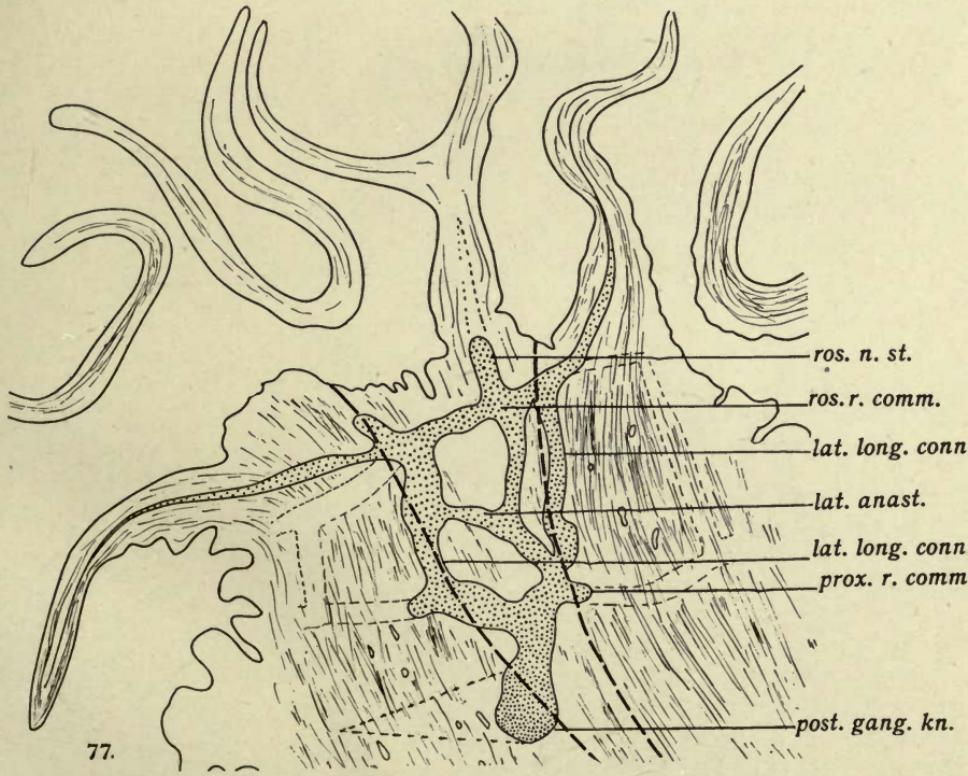
ros. r. comm.—rosette ring commissure.

ros. sphinc.—rosette sphincter.

tp.—tope.



76.



77.



PLATE 47.

Fig. 78. Nervous system of *Moniezia expansa*, after Tower (1900).

Fig. 79. Nervous system of Triclad; after Lang (1881).

Fig. 80. *G. nigrosetosa*, Haswell (1902, pl. VII, fig. 1).

Fig. 81. Same, egg, showing operculum. Haswell (1902, pl. VII, fig. 7).

ant. br. comm.—anterior bridge commissure.

ant. gang. kn.—anterior ganglion knot.

ant. r. comm.—anterior ring commissure.

dist. r. comm.—distal ring commissure.

lat. long. conn.—lateral longitudinal connective.

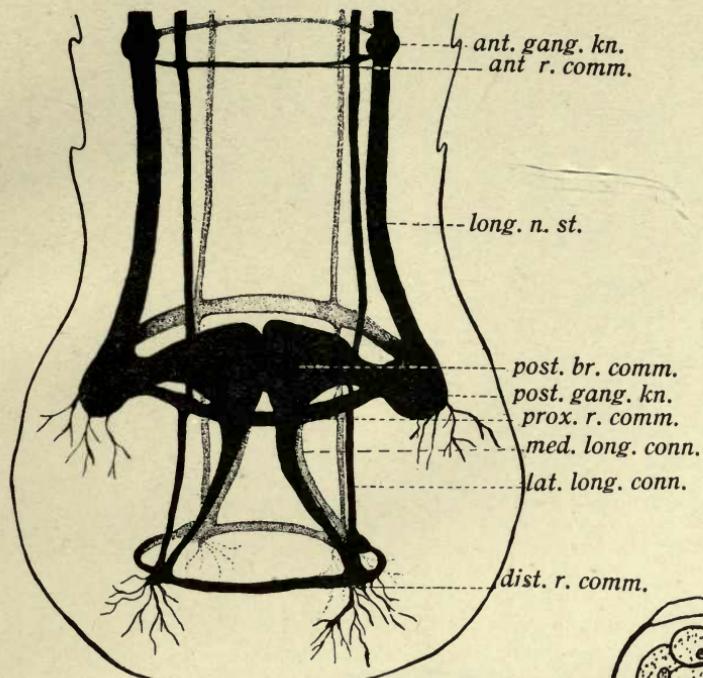
long. n. st.—longitudinal nerve stem.

med. long. conn.—median longitudinal connective.

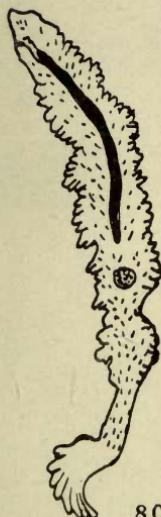
post. br. comm.—posterior bridge commissure.

post. gang. kn.—posterior ganglion knot.

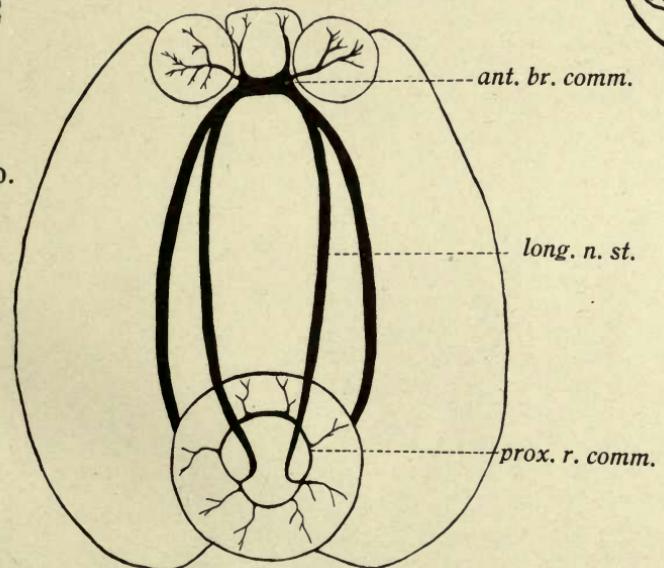
prox. r. comm.—proximal ring commissure.



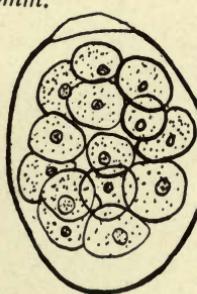
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80.



79.



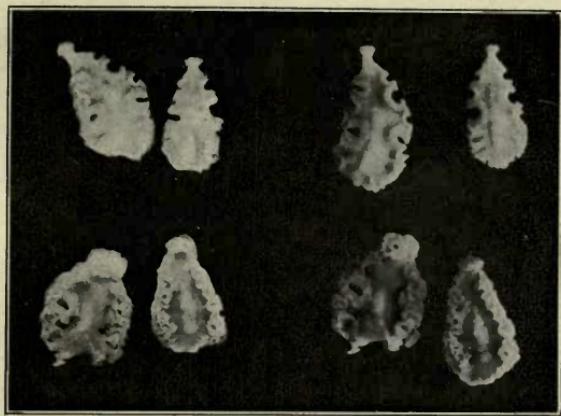
81.



PLATE 48.

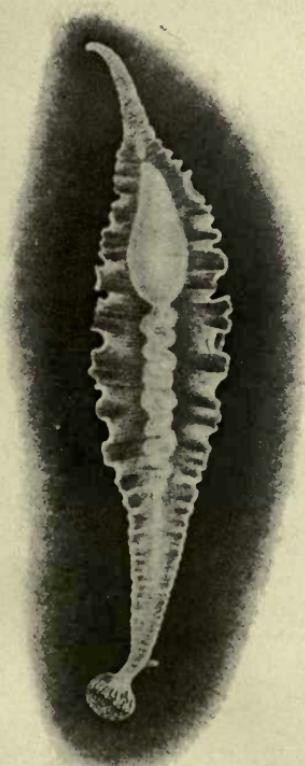
Figs. 82, 83. Photographs of living specimens of *G. fimbriata* and *G. urna* (var.) All in state of contraction. About natural size.

Figs. 84, 85. *G. urna*, from Wagener (1852, pl. 14, figs. 1, 2).

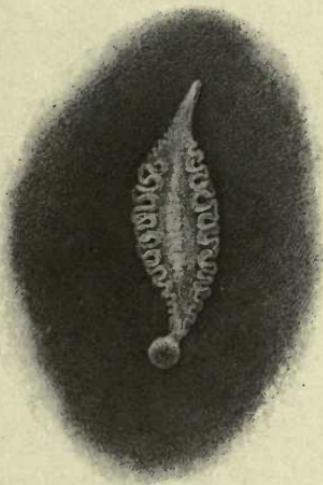


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85

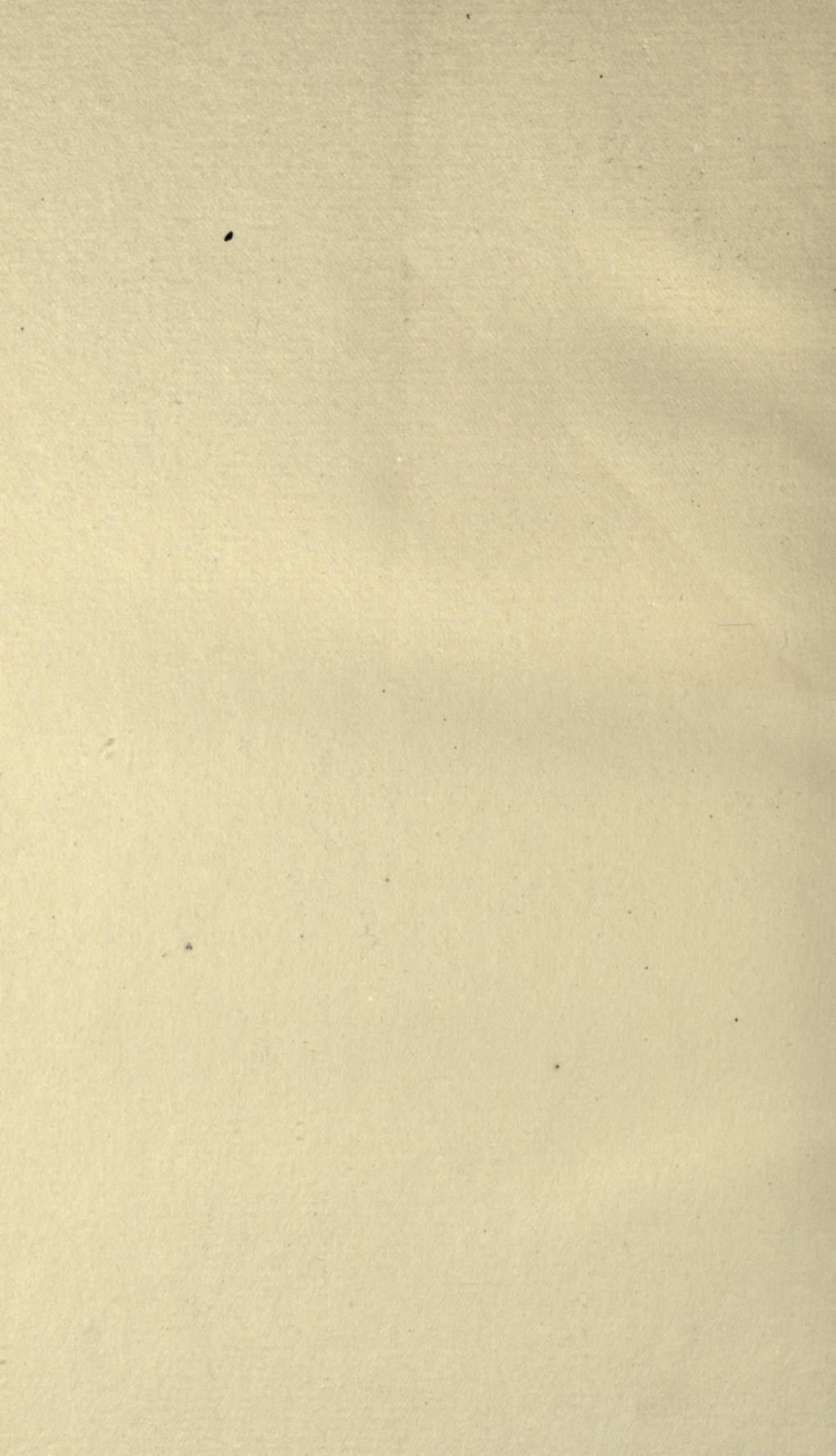
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